

Assessing the relative potential ecological impacts and invasion risks of emerging and future invasive alien species

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Abstract

Invasive alien species (IAS) cause myriad negative impacts, such as ecosystem disruption, human, animal and plant health issues, economic damage and species extinctions. There are many sources of emerging and future IAS, such as the poorly regulated international pet trade. However, we lack methodologies to predict the likely ecological impacts and invasion risks of such IAS which have little or no informative invasion history. This study develops the Relative Impact Potential (RIP) metric, a new measure of ecological impact that incorporates *per capita* functional responses (FRs) and proxies for numerical responses (NRs) associated with emerging invaders. Further, as propagule pressure is a determinant of invasion risk, we combine the new measure of Pet Propagule Pressure (PPP) with RIP to arrive at a second novel metric, Relative Invasion Risk (RIR). We present methods to calculate these metrics and to display

the outputs on intuitive bi- and triplots. We apply RIP/RIR to assess the potential ecological impacts and invasion risks of four commonly traded pet turtles that represent emerging IAS: *Trachemys scripta scripta*, the yellow-bellied slider; *T. s. troostii*, the Cumberland slider; *Sternotherus odoratus*, the common musk turtle; and *Kinosternon subrubrum*, the Eastern mud turtle. The high maximum feeding rate and high attack rate of *T. s. scripta*, combined with its numerical response proxies of lifespan and fecundity, gave it the highest impact potential. It was also the second most readily available according to our UK surveys, indicating a high invasion risk. Despite having the lowest maximum feeding rate and attack rate, *S. odoratus* has a high invasion risk due to high availability and we highlight this species as requiring monitoring. The RIP/RIR metrics offer two universally applicable methods to assess potential impacts and risks associated with emerging and future invaders in the pet trade and other sources of future IAS. These metrics highlight *T. s. scripta* as having high impact and invasion risk, corroborating its position on the EU list of 49 IAS of Union Concern. This suggests our methodology and metrics have great potential to direct future IAS policy decisions and management. This, however, relies on collation and generation of new data on alien species functional responses, numerical responses and their proxies, and imaginative measures of propagule pressure.

Keywords

ecological impacts, functional response, invasive alien species, numerical response, pet propagule pressure, relative impact potential, relative invasion risk, risk assessment

Introduction

Invasive alien species (IAS), i.e. those introduced to areas outside their native range (which may or may not then have impact; see Ricciardi and Cohen 2007), can be major drivers of global biodiversity loss and cause a range of other negative impacts (Tilman et al. 2017). While many species fail to establish, i.e. are not capable of reproducing and becoming self-sustaining populations, some do establish, spread and exert strong, negative ecological effects (Colautti et al. 2014; Dick et al. 2017a, b). Propagule pressure, the number, frequency and viability of individuals of each species released, is a key factor determining whether a species establishes, with the aquarium and ornamental trades shown to be a major determinant of propagule pressure (Gertzen et al. 2008; García-Díaz et al. 2015). This is deemed responsible for a third of aquatic IAS (Padilla and Williams 2004), due to poor industry regulation (Raghavan et al. 2013) and fuelled by misconceptions surrounding the ethics and consequences of “mercy” release (Liu et al. 2013). The global trade of reptiles and amphibians in particular has led to the spread of some high profile IAS with serious ecological impacts (Kraus 2015). The numbers of alien species introductions are unlikely to saturate in the near future (Seebens et al. 2018), but understanding, assessing and predicting the associated ecological impacts has proven difficult, especially for species without invasion histories. Some high profile failed attempts at controlling IAS (Courchamp et al. 1999; Rayner et al. 2007) have led to a consensus being reached that prevention is the best option for IAS management (Piria et al. 2017). However, prevention strategies require new methods to quantify likely ecological impact, here defined as negatively affecting the

abundance of one or more native species, and invasion risk, which combines impact with likelihood of establishment, for emerging and potential future invaders (Dick et al. 2017b).

Comparative functional responses (CFRs) have been successful in characterising damaging IAS and have proven predictive for those without invasion impact history (Dick et al. 2014, 2017b). CFR can also take into account a wealth of context-dependencies and interactive effects, such as dissolved oxygen levels (Lavery et al. 2015), habitat complexity (Wasserman et al. 2016), temperature (Xu et al. 2016; Cuthbert et al. 2018), higher order predators (Barrios-O'Neill et al. 2014) and presence of parasites (Lavery et al. 2017b). However, despite the many advantages of the CFR methodology, the impacts of a consumer on resources (e.g. predator on prey) will clearly be the product of these *per capita* effects and the population response of the consumer (i.e. the numerical response (NR); Solomon, 1949). A simpler proxy for NR is the abundance of a species, which has recently been combined with CFR into the Relative Impact Potential (RIP) metric to successfully predict invader ecological impact (Dick et al. 2017b).

RIP might prove particularly valuable for the study of IAS emerging from the pet trade, with global trade of freshwater turtles in particular a pressing problem (Nori et al. 2017). For example, *Trachemys scripta elegans* (the red-eared slider) appears both on the EU List of IAS of Union concern and the IUCN's 100 Worst Invasive Species list, having invaded 73 countries (García-Díaz et al. 2015; Capinha et al. 2017) and living on every continent except Antarctica (Rödder et al. 2009). This species was once widely traded due to its small size as juveniles, ease of maintenance, relative affordability (Teillac-Deschamps et al. 2009) and, remarkably, the global craze of Teenage Mutant Ninja Turtles (Somma et al. 2009a). Upon release, *T. s. elegans* has been shown to compete with native turtles for food and basking habitat (Cadi and Joly 2003; Pearson et al. 2015). We thus urgently require methods to predict the impacts of these and similar potential IAS that currently lack both invasion history and invasion range population abundance data.

Here, we utilise the RIP metric and biplots of Dick et al. (2017b) and Lavery et al. (2017b) and develop these with alternative available proxies for the numerical response, namely "lifespan", "fecundity" and their product, "lifetime fecundity". These proxies may not necessarily be accurate reflections of the numerical response *per se*, but rather are useful for comparative purposes, as were abundance and biomass in the original RIP metric (Dick et al. 2017b). Unlike the true numerical response and even abundance/biomass (see Dick et al. 2017b), the three measures above are generally available in literature for most species and are so for the current study species. Further, as fecundity is clearly linked to the numerical response and lifespan may determine ecological impact over time, these proxies, in a comparative sense, are useful multipliers of *per capita* effects (see Dick et al. 2017b). Also included in the present study is the functional response "attack rate", which offers insights into predatory impact at low prey densities (i.e. destabilising Type II FRs), as well as the "maximum feeding rate", calculated as the reciprocal of the "handling time" (Dick et al. 2017b). Since prop-

agule pressure is a major determinant of invasion risk (Briski et al. 2012) and possibly impact (Ricciardi and Cohen 2007), we further modify the RIP biplots of Lavery et al. (2017b) to include propagule pressure on a third axis (i.e. triplots) to give a combined measure of Relative Invasion Risk (RIR). Using these metrics, we investigate the relative potential ecological impacts and invasion risks of four commonly traded freshwater turtles: two *Trachemys scripta* subspecies that have recently been added to the EU list of 49 IAS of Union Concern, namely *T. s. scripta*, the yellow-bellied slider and *T. s. troostii*, the Cumberland slider; as well as *Sternotherus odoratus*, the common musk turtle and *Kinosternon subrubrum*, the Eastern mud turtle, both of which are also widely available in the pet trade.

Methods

Study species

Trachemys scripta scripta, *T. s. troostii*, *Sternotherus odoratus* and *Kinosternon subrubrum* originate from North America and are sold around the world (Polo-Cavia et al. 2011), with *T. scripta* and *S. odoratus* being amongst the most commonly imported turtle species into the UK and Ireland (García-Díaz et al. 2014). Their longevity and lack of predators and competitors mean that, even if current environmental conditions prevent reproduction in some of their introduced ranges, there is the potential for ecological impact and invasion risk. This may be exacerbated if climate change and/or adaptation leads to these populations becoming viable (Bugter et al. 2011).

T. s. scripta and *T. s. troostii* can live for 36 years (Frazer et al. 1990) and reproduction is expected to be similar to *T. s. elegans*, with females laying up to five clutches per year, with between 2 and 23 eggs in each clutch (Somma et al. 2009a). *Sternotherus odoratus* can live for 30 years (Bugter et al. 2011), with females laying 2 to 4 clutches per year, with between 1 and 9 eggs per clutch (Somma and Fuller 2009). *Kinosternon subrubrum* can live for 46 years (Frazer et al. 1990) and females tend to lay between 1 and 3 clutches per year, with 1 to 6 eggs per clutch (Somma et al. 2009b).

Animal collection and maintenance

The four turtle species were provided by Maidenhead Aquatics, Northern Ireland (carapace lengths 35–50 mm; mixed sexes) and maintained in holding tanks containing a water heater (150W Eheim thermocontrol, Germany) and water cooler to ensure water temperature was maintained at 16 °C. Two basking platforms and basking lights created a hot spot of 23 °C, controlled by an automatic temperature controller (Habitat Classic, England). Substrate (0.8 mm grain size) was added to the bottom 30 mm of each holding tank (JBL, Germany). Nine individuals of each species were acquired for each experimental batch and each species received its own holding tank and was

quarantined for one week prior to experiments. During this period, no illness or deaths were recorded and the animals were fed daily with commercial floating turtle food (JBL, Germany). Before experimental FR trials, all turtles were starved for 24 hours to standardise hunger levels. Focal prey, the amphipod crustacean *Gammarus pulex* (15–17 mm body length; unparasitised), upon which all turtle species were observed to feed readily and represents a general prey item, were collected from the Minnowburn River, N. Ireland (N54.546, W5.594) two days before the experiments and acclimatised to the experimental temperature.

FR procedure

Experiments were performed 22 February–27 April 2016. Experimental tanks (250 mm × 120 mm × 90 mm) with 30 mm of substrate at 16 °C were supplied with prey 15 minutes prior to the turtles being introduced. Prey densities were 2, 4, 8, 16, 32, 64, 128, 256 ($n = 6$ per experimental group). For each turtle species, individuals were randomly selected and assigned to a random prey density and allowed to feed for thirty minutes. Controls were performed for each prey density ($n = 3$ each) with the same experimental conditions but in the absence of turtle predators, to quantify prey mortality for any other reasons.

Statistical methods

Data were analysed using R version 3.2.3. (R Core Team 2015). Logistic regression of the proportion of prey killed as a function of prey density was used to discern functional response types (see Juliano 2001). Where a significant negative first order linear coefficient was detected, a Type II response was ascribed; conversely, a Type III form was considered when a significant positive first order linear coefficient was followed by a significant negative second order coefficient (Juliano 2001). Rogers' random predator equation for non-replacement of prey was applied to estimate values of ' h ' (handling time) and ' a ' (attack rate):

$$N_e = N_o(1 - \exp(-a(N_e h - T))) \quad (1)$$

where N_e is the number of prey eaten, N_o is the initial density of prey, h is the handling time, a is the attack constant and T is the total experimental period. Model fitting used the Lambert W function (Bolker 2008) in R due to the implicit nature of the random predator equation. This relates to the fact that the random predator equation is not solvable on its own and requires the Lambert W function for this. See the opening paragraph of <https://ms.mcmaster.ca/~bolker/misc/rogers2.pdf>. Data were bootstrapped ($n = 30$) to calculate multiple estimates of the handling time h , maximum feeding rate ($1/h$) and attack rate a with standard error (SE).

Metrics and measures

Relative Impact Potential (RIP) was originally developed using population abundance/density/biomass as a proxy for the consumer numerical response (NR: Dick et al. 2017b), but in certain situations such data are lacking, as, for example, with potential future invasions by turtles and other potential IAS. Since our metrics are comparative rather than absolute, we substituted the NR with other life history measures of the invaders that may influence impact. Here, we thus propose three other alternative proxies for the numerical response:

(1) *Lifespan* (L). With temperatures in many temperate regions high enough for turtles to survive in the wild for many years, but as yet too low to facilitate reproduction (Teillac-Deschamps et al. 2009; but see Standfuss et al. 2016), lifespan offers a proxy multiplier of *per capita* effects (when other proxies such as abundance are not available), giving a metric quantifying the ecological impact that a species may exert over space and time. Thus, Impact Potential utilising lifespan data (IP_L) is:

$$IP_L = FR \times L \quad (2)$$

where FR is the functional response (estimated maximum feeding rate, $1/h$, from equation 1) and L is maximum lifespan (Table 1);

(2) *Fecundity* (F). Where reproduction of the turtles occurs or may occur in future, fecundity offers another proxy multiplier of *per capita* effects, since reproductive output is clearly an element of the true numerical response. Thus, Impact Potential utilising fecundity data (IP_F) is:

$$IP_F = FR \times F \quad (3)$$

where FR is as above and F is the product of clutch size and number of clutches per annum (Table 1);

(3) *Lifetime fecundity* (LF). Where suitable data are available, a third proxy for the numerical response may be constructed as the product of maximum lifespan and fecundity, that is lifetime fecundity (LF), as this captures both reproductive output per bout and over time and thus Impact Potential is:

$$IP_{LF} = FR \times LF \quad (4)$$

The RIP calculations of Dick et al. (2017b) and RIP biplots of Lavery et al. (2017b) use maximum feeding rate ($1/h$) as the FR measure (see above), based on the curve parameter “*h*” (handling time). Here, we propose the additional use of the other classic FR parameter, “*a*” (attack rate), since this quantifies the initial gradient of the

Table 1. Numerical response proxies of lifespan, fecundity and lifetime fecundity, plus Pet Propagule Pressure (PPP; see Text and Table 3) for our study turtle species. Pet Propagule Pressure (Northern Ireland, NI) is a function of the proportional availability of each species across pet shops and the total number of pet shops surveyed and PPP (Great Britain, GB) is the proportional availability of the four species based on online classified advertisements and the total number of online advertisements surveyed.

Turtle	Lifespan (L) (maximum years)	Ref.	Fecundity (F) (eggs per year)	Ref.	Lifetime fecundity (LxF)	Pet Prop. Press. (PPP _{NI})	Pet Prop. Press. (PPP _{GB})
<i>T. s. scripta</i>	36	Frazer et al. 1990	115	Somma et al. (2009a)	4140	0.05	0.1
<i>T. s. troostii</i>	36	Frazer et al. 1990	115	Somma et al. (2009a)	4140	0.00	0.05
<i>S. odoratus</i>	30	Bugter et al. 2011	36	Somma and Fuller (2009)	1080	0.30	0.39
<i>K. subrubrum</i>	46	Frazer et al. 1991	18	Somma et al. (2009b)	828	0.05	0.02

functional response curve, giving insights into the critical population level impact that a consumer can exert at low resource densities (Dick et al. 2014). Thus, Impact Potential utilising attack rate and lifespan data (IP_L) is:

$$IP_L = a \times L \quad (5)$$

and with fecundity data is:

$$IP_F = a \times F \quad (6)$$

and with lifetime fecundity:

$$IP_{LF} = a \times LF \quad (7)$$

In addition, to enter the propagule pressure argument to measure overall invasion risk, we qualify each IP equation with Pet Propagule Pressure (PPP). We propose two PPP methods. First, we quantified the availability of the four species on a local (i.e. Northern Ireland, NI) level *via* a survey of twenty pet shops between the 31 January and 1 March 2017 (Suppl. material 1: Table S1; PPP values as per Table 1). PPP in this context is calculated as follows:

$$PPP(NI) = Np/Tp \quad (8)$$

where Pet Propagule Pressure (Northern Ireland, NI) is a function of the proportional availability of each species across pet shops (Np) and the total number of pet shops surveyed (Tp).

The second version of PPP involved a survey of online classified advertisements (Suppl. material 2: Table S2; PPP values as per Table 1). A major advantage of this method is that each advertisement represents an unwanted pet, a key feature of pet releases into the wild. This second survey was conducted on 21 November 2017 and used two websites, www.preloved.co.uk and www.pets4homes.co.uk. Search terms of

‘terrapin’ and ‘turtle’ were used for both websites and screenshots were taken of each advertisement claiming to be selling our study species. Using the location of the seller and the screenshot images, we prevented the double-counting of advertisements. The PPP values were calculated as follows:

$$PPP(GB) = Na/Ta \quad (9)$$

where PPP (Great Britain, GB) is the proportional availability of the four species based on online classified advertisements (Na) and the total number of online advertisements surveyed (Ta).

By incorporating these two measures of propagule pressure, the Impact Potential (IP) equations (equations 2–7) can incorporate both risk of introduction and its ecological consequences to become Invasion Risk (IR):

$$IR_L = FR \times L \times PPP \quad (10)$$

$$IR_F = FR \times F \times PPP \quad (11)$$

$$IR_{LF} = FR \times LF \times PPP \quad (12)$$

$$IR_L = a \times L \times PPP \quad (13)$$

$$IR_F = a \times F \times PPP \quad (14)$$

$$IR_{LF} = a \times LF \times PPP \quad (15)$$

We present biplots to illustrate Relative Impact Potential (equations 2–7) and triplots for Relative Invasion Risk (equations 10–15) of the four turtle species to give visual representations of relative ecological impact and invasion risk (see Suppl. material 3, 4 for R scripts, and Suppl. material 5 for associated .csv file).

Results

Prey survival in control treatments was 98–100%, therefore mortality during FR experiments was attributed to predation, which was also directly observed. Type II functional responses were observed for all turtle species (Table 2; Figure 1). Handling times were lowest and, hence, maximum feeding rates were highest, for the two *T. scripta* subspecies, with the order *T. s. scripta* > *T. s. troostii* > *K. subrubrum* > *S. odoratus* (Fig. 2a, b). *T. s. scripta* had the highest attack rate, *S. odoratus* the lowest and *T. s. troostii* and *K. subrubrum* were intermediate (Fig. 2c), with *K. subrubrum* having a higher attack rate, but also higher handling time (i.e. lower maximum feeding rate) than *T. s. troostii* (Fig. 2a–c).

Table 2. First order terms calculated from logistic regression to denote functional response type across all predator treatments. The significant negative first order term values across all four turtles indicate Type II functional responses for each predator. Handling time (h), maximum feeding rate ($1/h$) and attack rate (a) parameter mean estimates (bootstrapped, $n = 30$), derived using Rogers' random predator equation (eqn 1).

Predator	First term, P	Handling time, h	Maximum feeding rate, $1/h$ (<i>G. pulex</i> consumed per 30 mins)	Attack rate, a
<i>T. s. scripta</i>	-0.011, <0.001	0.027	37.036	2.678
<i>T. s. troostii</i>	-0.011, <0.001	0.028	35.405	2.038
<i>S. odoratus</i>	-0.011, <0.001	0.039	25.468	1.847
<i>K. subrubrum</i>	-0.012, <0.001	0.037	27.142	2.314

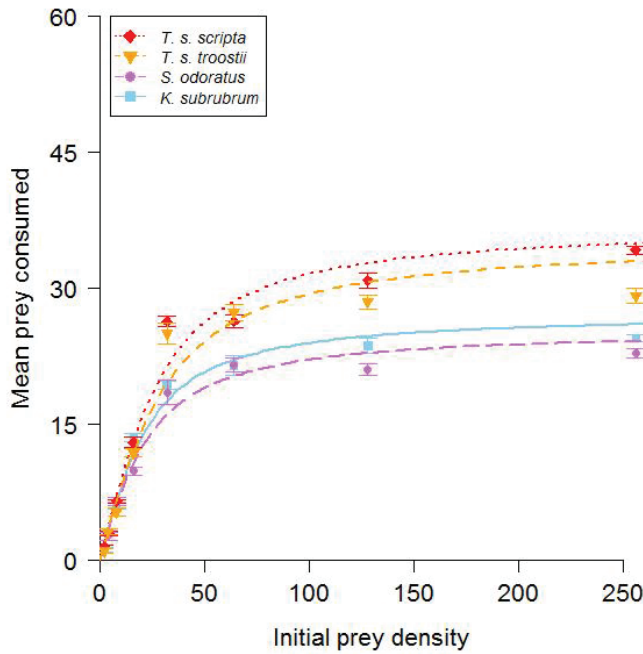


Figure 1. Functional responses of *T. s. scripta*, *T. s. troostii*, *S. odoratus* and *K. subrubrum* towards *G. pulex* prey. Values are mean $\pm$ SE.

The numerical response proxy values are given in Table 1 and the IP and IR values in Table 3. Impact Potential (IP) scores using maximum feeding rate (see Tables 2, 3) with all three numerical response proxies were higher for *T. s. scripta* and *T. s. troostii* relative to *K. subrubrum* and *S. odoratus* (equations 2–4; Table 3; Fig. 3a–c). However, when attack rate was used with lifespan, the IP score was highest for *K. subrubrum*, closely followed by *T. s. scripta* and *T. s. troostii* and then *S. odoratus* (equation 5; Table 3; Fig. 3d). If we consider fecundity and lifetime fecundity, IP was again highest for *T. s. scripta* and *T. s. troostii* versus *S. odoratus* and *K. subrubrum*, which were similar (equation 6, 7; Table 3; Fig. 3e, f).

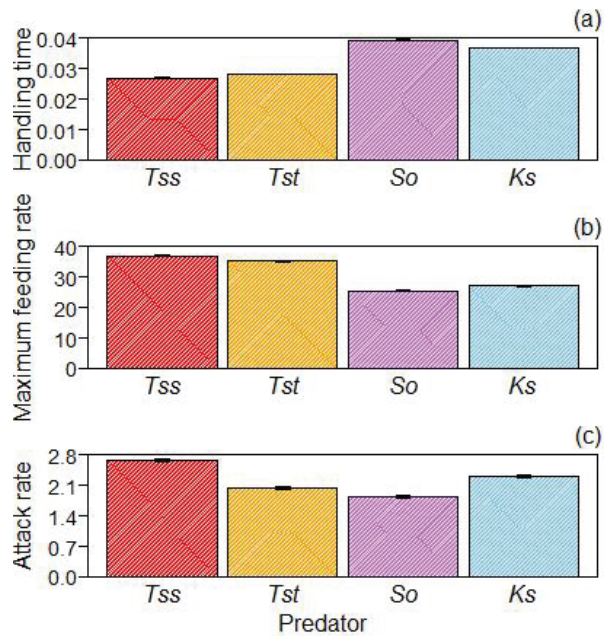


Figure 2. Parameter estimates ($\pm$ SE) of: **a** handling time **b** maximum feeding rate $1/h$ **c** attack rate a , for bootstrapped ($n = 30$) Type II functional response curves of *T. s. scripta* (Tss), *T. s. troostii* (Tst), *S. odoratus* (So) and *K. subrubrum* (Ks) towards *G. pulex* prey.

Table 3. Impact Potential (IP) and Invasion Risk (IR) calculations, whereby: $IP(FR) = \text{Maximum feeding rate (FR)} \times \text{NRproxy i.e. lifespan (L), fecundity (F) or lifetime fecundity (LF)}$; $IP(a) = \text{Attack rate (a)} \times \text{NRproxy}$; $IR(FR) = IP(FR) \times \text{Pet Propagule Pressure (PPP)}$; $IR(a) = IP(a) \times \text{PPP}$. PPP_{NI} (Northern Ireland) is a function of the proportional availability of each species across pet shops and the total number of pet shops surveyed and PPP_{GB} (Great Britain) is the proportional availability of the four species based on online advertisements and the total number of advertisements surveyed.

	$IP_L(FR)$	$IP_F(FR)$	$IP_{LF}(FR)$	$IP_L(a)$	$IP_F(a)$	$IP_{LF}(a)$
<i>T. s. scripta</i>	1,333.30	4,259.14	153,329.04	96.41	307.97	11,086.92
<i>T. s. troostii</i>	1,274.76	4,072.15	146,597.40	73.37	234.37	8,437.32
<i>S. odoratus</i>	764.04	916.85	27,505.44	55.41	66.49	1,994.76
<i>K. subrubrum</i>	1,248.53	488.56	22,473.58	106.44	41.65	1,915.99
Using PPP_{NI}	$IR_L(FR)$	$IR_F(FR)$	$IR_{LF}(FR)$	$IR_L(a)$	$IR_F(a)$	$IR_{LF}(a)$
<i>T. s. scripta</i>	66.66	212.96	7,666.45	4.82	15.40	554.35
<i>T. s. troostii</i>	0	0	0	0	0	0
<i>S. odoratus</i>	229.21	275.05	8,251.63	16.62	19.95	598.43
<i>K. subrubrum</i>	62.43	24.43	1,123.68	5.32	2.08	95.80
Using PPP_{GB}	$IR_L(FR)$	$IR_F(FR)$	$IR_{LF}(FR)$	$IR_L(a)$	$IR_F(a)$	$IR_{LF}(a)$
<i>T. s. scripta</i>	133.33	425.91	15,332.90	9.64	30.80	1,108.69
<i>T. s. troostii</i>	63.74	203.61	7,329.87	3.67	11.72	421.87
<i>S. odoratus</i>	297.98	357.57	10,727.12	21.61	25.93	777.96
<i>K. subrubrum</i>	24.97	9.77	449.47	2.13	0.83	38.32

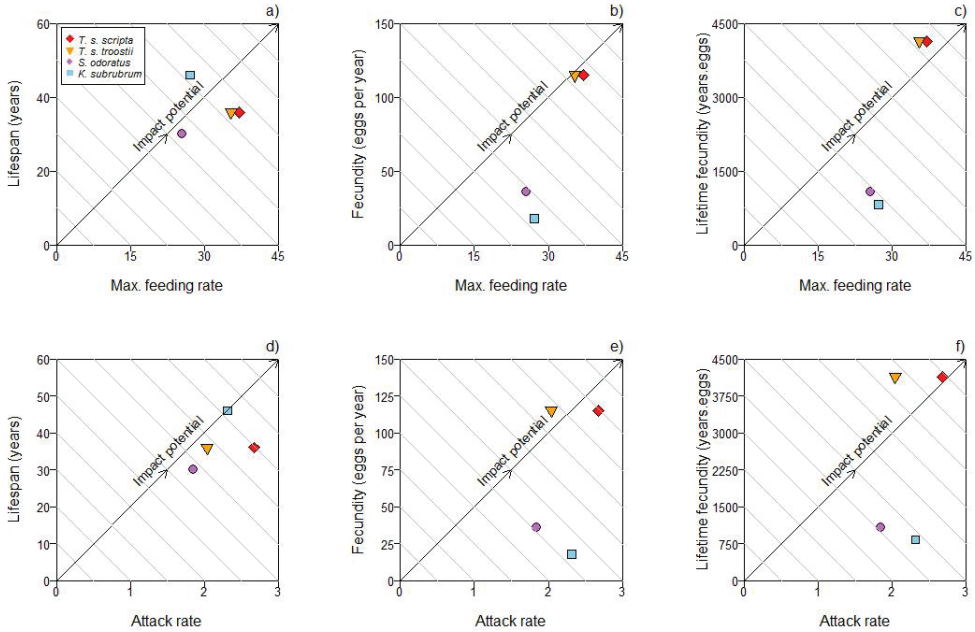


Figure 3. Biplots showing Relative Impact Potential of *T. s. scripta*, *T. s. troostii*, *S. odoratus* and *K. subrubrum* towards *G. pulex* prey. Impact potential calculated as a product of maximum feeding rate and lifespan (a), fecundity (b) and lifetime fecundity (c); then attack rate and lifespan (d), fecundity (e) and lifetime fecundity (f). Impact increases from bottom left to top right.

Pet Propagule Pressure (PPP) of each species was similar in both the Northern Ireland (NI) and Great Britain (GB) surveys, with respective orders of *S. odoratus* > *T. s. scripta* = *K. subrubrum* > *T. s. troostii* and *S. odoratus* > *T. s. scripta* > *T. s. troostii* > *K. subrubrum* (see Table 1 and details of the two surveys are outlined in Suppl. material 1: Table S1 and Suppl. material 2: Table S2).

For all six of the NI Relative Invasion Risk (RIR) triplots, values were highest for *S. odoratus*, with the order *S. odoratus* > *T. s. scripta* > *K. subrubrum* > *T. s. troostii* across all derivations of RIR (equations 10–15; Table 3; Fig. 4a–f). For the GB RIR triplots, the order using both lifespan calculations was *S. odoratus* > *T. s. scripta* > *T. s. troostii* > *K. subrubrum* (Fig. 5a, d), but for all other RIR metrics, the order was *T. s. scripta* > *S. odoratus* > *T. s. troostii* > *K. subrubrum* (equations 10–15; Table 3; Fig. 5b, c, e, f).

Discussion

Invasion ecology has long lacked a unifying methodology that predicts ecological impacts and overall invasion risks of invasive species (Dick et al. 2017a). Propagule pressure alone is often unable to incorporate context-dependencies (Dick et al. 2017a)

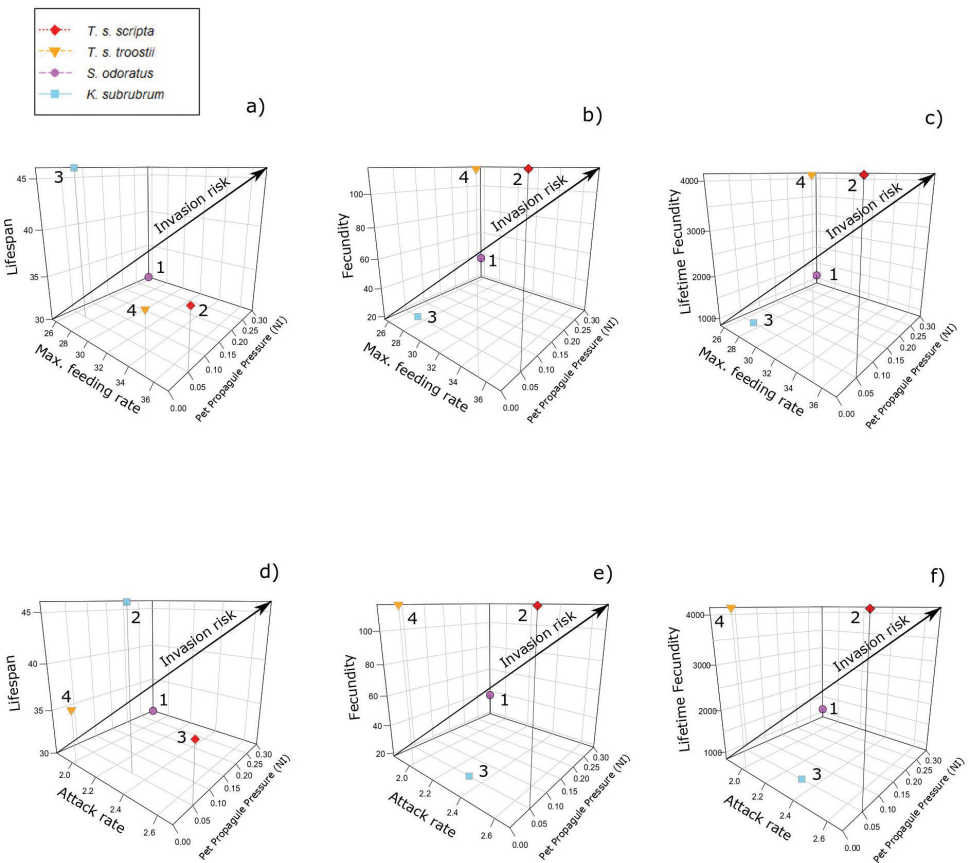


Figure 4. Triplots showing Relative Invasion Risk of *T. s. scripta*, *T. s. troostii*, *S. odoratus* and *K. subrubrum* in a Northern Irish context. Invasion Risk calculated as a product of maximum feeding rate and Pet Propagule Pressure (PPP) with lifespan (a), with fecundity (b) and with lifetime fecundity (c); then attack rate and PPP with lifespan (d), with fecundity (e) and with lifetime fecundity (f). PPP for each species calculated by surveying 20 local pet shops and determining proportions of each species sold. Invasion Risk increases from bottom left to top right of each plot, with species ranked 1–4.

and invasion history is not always available for emerging and potential future invaders (Kulhanek et al. 2011). Furthermore, no single species trait or combination of traits offers consistent predictive efficacy (Ricciardi et al. 2013), although comparative functional responses (CFR) have, up until now, given the most effective predictions of invader ecological impact across a wide range of abiotic and biotic contexts (Dick et al. 2014, 2017b). These relationships between resource availability and resource uptake rate have proven robust in comparing invaders with trophically analogous natives or other invaders, even in laboratory conditions that do not necessarily mimic natural conditions (Lavery et al. 2017b). Here, we found that each turtle species followed classic Type II functional responses, whereby, at low prey densities, high proportions of prey are consumed and hence prey populations may be destabilised. Thus, the

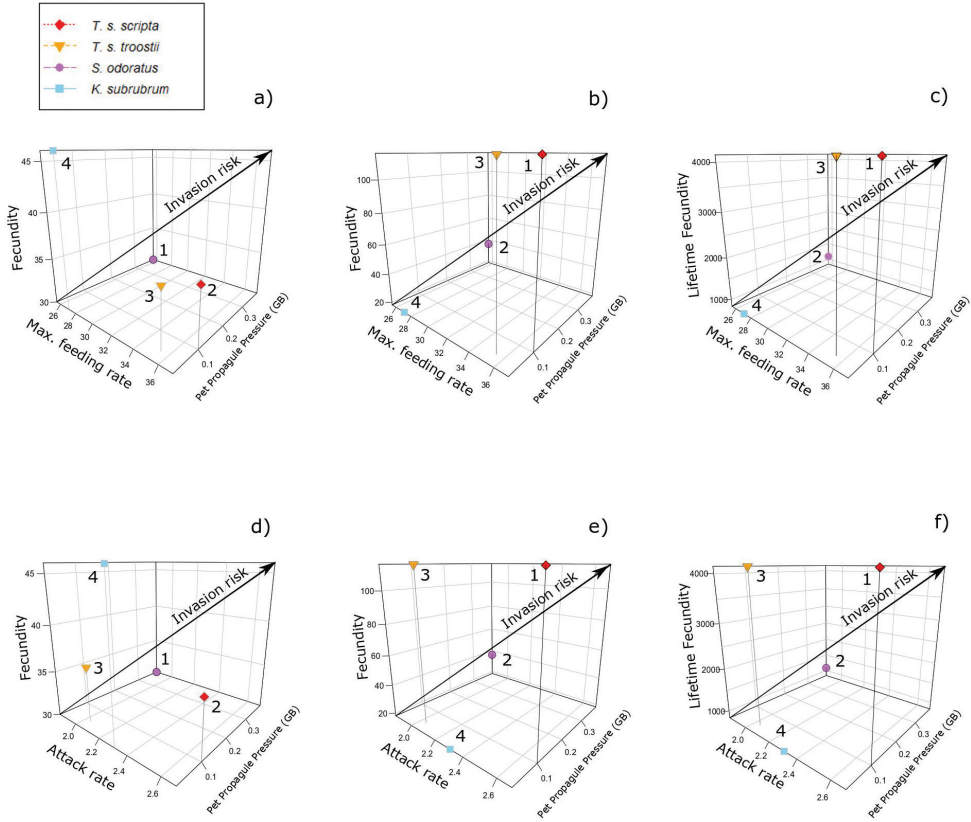


Figure 5. Triplots showing Relative Invasion Risk of *T. s. scripta*, *T. s. troostii*, *S. odoratus* and *K. subrubrum* in a Great British context. Invasion Risk is calculated as a product of maximum feeding rate, lifespan and Pet Propagule Pressure (PPP) (a), with fecundity (b) and with lifetime fecundity (c); then attack rate, lifespan and PPP (d), with fecundity (e) and with lifetime fecundity (f). PPP for each species calculated by surveying classified advertisements online and finding what proportion were selling the species in question. Invasion Risk increases from bottom left to top right of each plot, with species ranked 1–4.

introduction, establishment and spread of alien turtles could have marked top-down impacts on aquatic fauna in freshwater ecosystems. We predict that *T. s. scripta* and *T. s. troostii* will have the greatest ecological impacts. The two *T. scripta* subspecies were shown to have the highest maximum feeding rates, with *T. s. scripta* and *K. subrubrum* shown to have the highest attack rates, an indication of impact at low prey densities. *T. s. scripta* displayed a “perfect storm” of highest maximum feeding rates and highest attack rates, suggesting potential for significant impacts upon freshwater invertebrate communities.

While FR analyses have been used mainly to determine the impacts of alien predators (see Dick et al. 2014; Alexander et al. 2014; Dick et al. 2017b), they may also be used to assess impacts of herbivores (e.g. Xu et al. 2016) or any other trophic/taxonomic group (Dick et al. 2014). Additionally, FRs can inform about the competitive abili-

ties of species and, indeed, competition theory was heavily based on the “functional resource-utilisation responses” of plants (see Tilman 1977; Dick et al. 2017a). While the use of comparative FRs in assessing inter-specific competition amongst animal taxa has been slow in its adoption, we foresee development of this method and our metrics to assess ecological impact through competition, as occurs between alien and native turtles (Cadi and Joli 2003; Polo-Cavia et al. 2011).

The Impact Potential (IP) and Invasion Risk (IR) metrics, plus our illustrative bi- and triplots giving Relative IP and Relative IR, retain the benefits of CFR, but bolster these *per capita* measures with proxies for the numerical response (NR), that is, the consumer population response. Emerging invaders may lack NR data and have no data for their abundances/densities/biomass in potential invasion regions. With these latter NR proxies not available, we hence require alternatives and use lifespan, fecundity and lifetime fecundity as comparative multipliers of *per capita* effects. The resulting impact potentials were subsequently combined with values for our two versions of Pet Propagule Pressure (PPP) to give Invasion Risk (IR), which assesses which species are currently the most likely candidates for introduction, combined with potential impact. Using these approaches, we determined that *T. s. scripta* and *T. s. troostii* have the highest RIP, but the more commonly traded *S. odoratus* has the greatest RIR and thus should be of great concern. Our approach illustrates the potential use of combinatorial metrics to guide policy and intervention and exploits inherent life-history traits of invaders with their feeding impacts and their likelihood of introduction.

The use of maximum lifespan as a numerical response proxy offers a readily available multiplier of *per capita* effects. With reproduction by these turtles not yet possible in most temperate regions, the longer the species survive in the wild, the greater the ecological impact that will accrue. One caveat is the combination of unfamiliar climate, flora and fauna, combined with invader naiveté, which could alter the estimations of lifespan should these species be released into the wild. A caveat exists for lifetime fecundity too, as fecundity does not remain constant over the course of a lifetime. However, as our metric is comparative and all species should be equally affected, such reductions may not affect predictions of relative ecological impact. Here, using lifespan, we find that *T. s. scripta* and *T. s. troostii* had the highest impact potentials on the maximum feeding rate biplot, while *K. subrubrum* and *T. s. scripta* had the highest and second highest impacts on the attack rate biplot. However, as illustrated by Dick et al. (2017b), it is maximum feeding rate combined with NR proxies that give highest success in ecological impact prediction and hence we conclude here that *T. s. scripta* and *T. s. troostii* will have the greatest ecological impacts as invaders.

Our second NR proxy, fecundity, defined as the number of offspring born over a given period of time (Lamb et al. 2009), can be a key determinant of whether or not an introduced population establishes and subsequently persists (Pöckl 2007). The inability to reproduce in northern European climates has dampened the impact of *T. scripta elegans*, but where this barrier to reproduction does not apply, this and other introduced reptiles have strong impacts (Kraus 2015). Our biplots illustrate the two *T. scripta* subspecies having the highest of such impact values, with the higher maximum

feeding rate and attack rate of *T. s. scripta* indicative of higher impact at both high and low prey densities. Our third NR proxy, lifetime fecundity, clearly distinguished the two *T. scripta* subspecies from the other turtles, with *T. s. scripta* having the greatest potential impact.

Our novel Relative Invasion Risk (RIR) triplots used Pet Propagule Pressure (PPP) to give a third dimension for invasion risk assessment. The first PPP calculations are based on a survey of 20 pet shops, ranging from small independent traders to UK-wide chains across Northern Ireland (NI). This offered vital data on which species are currently being sold in the NI pet trade and, by proxy, which species are likely candidates for future release and escape (Bugter et al. 2011). Pet shop availability has previously been used as an indicator of propagule pressure (Rixon et al. 2005; Gertzen et al. 2008), but the combination of this measure with impact potential allows users to counteract the shortcomings of propagule pressure for invasion risk prediction on its own (Dick et al. 2017a). Our survey found that *S. odoratus* was the most readily available of the four, with *K. subrubrum* and *T. s. scripta* featuring rarely. *T. s. troostii*, acquired for the study in the prior year, was not found in the survey. From all six of the triplots, the prevalence of *S. odoratus* in NI gave it the highest RIR of the four species, with all of the NR proxies and both maximum feeding rate and attack rate parameters. *T. s. scripta* came second to *S. odoratus* in all contexts with the exception of attack rate-lifespan, for which *K. subrubrum* had the second highest RIR.

The second measure of PPP was derived from online classified advertisements for unwanted pet turtles in GB and showed a similar result to that of the NI pet shop survey, with *S. odoratus* again found to be much more available than the other three turtle species. *S. odoratus* had the highest RIR for the lifespan calculations, but *T. s. scripta*, found to be twice as common in GB as it was in NI, had the highest RIR when fecundity and lifetime fecundity were taken into account. *Trachemys scripta troostii* was also more available than in the prior NI survey and, as a result, poses a greater risk in GB. Monitoring needs to occur in the future as changes in supply and demand will lead to the study species shifting their relative availabilities (Kitowski and Pachol 2009) and, as a result, RIR. Indeed, this novel metric illustrates the need to reduce propagule pressure driven by the pet trade and private holdings of such species.

Gertzen et al. (2008) cited size and aggression as major reasons for fish releases and similarly ownership difficulty was found to be a key determinant for establishment success of exotic reptiles (Fujisaki et al. 2010; García-Díaz et al. 2015). *T. scripta* spp. have been shown to be aggressively territorial (Polo-Cavia et al. 2011), with males reaching sizes of up to 24 cm and females 29 cm (van Dijk et al. 2011). Though smaller, *S. odoratus* still reach 14 cm (van Dijk 2015) and *K. subrubrum* 12 cm (van Dijk 2011). The likelihood of outgrowing their tanks, combined with longevity and their use in religious ceremonial release (Liu et al. 2013), suggests that all four are likely candidates for release.

Assessing potential for long-term impact requires information on which species will likely establish. Temperature is crucial for embryonic development and offspring phenotype (Booth 2006) and there are two types of temperature-dependent sex de-

termination (TSD). Species with TSD II, female-male-female, might have an invasion advantage, producing females at both cool and warm temperatures with males at intermediate temperatures (Ewert et al. 1994). *S. odoratus* has TSD II, with the lowest pivotal temperature at 20–21 °C (Bugter et al. 2011), whereas the *T. scripta* subspecies exhibit TSD Ia, male-female, with the sole pivotal temperature of 29–29.5 °C (Wibbels et al. 1998). However, potential to adapt to local thermal conditions (Zhao et al. 2015) and maternal behaviour buffering environmental conditions (Jackson 1988) highlight the need for effective monitoring across Europe.

The Relative Impact Potential metric, in its original form (Dick et al. 2017b), was based on the total response equation, i.e. the product of functional and numerical responses. With the complexity of calculating numerical responses well documented, using proxies of population abundance, density or biomass has been suggested (Dick et al. 2017b). In situations where such data are lacking, or inappropriate, such as when a species has no invasion history and using native population abundance could be misleading, there is a need to find other numerical response proxies. While we addressed longevity and fecundity, alternatives exist, for example, climatic similarity between native and potential invaded ranges (Filz et al. 2018), age of sexual maturity, embryological development time and number of generations per year (Grabowski et al. 2007). Further, embryonic development and hence key life history traits can be affected by toxicants (Zi et al. 2018), with the potential for such effects to vary amongst invaders and natives. We also highlight the potential for alternative proxies for propagule pressure, with the two methods applied here appropriate for species already available in the pet trade of the recipient area, but of limited use for those yet to arrive. We open the metric to alternative sources such as the US Law Enforcement Management Information System (LEMIS) database which records live wildlife imports and exports (Fujisaki et al. 2010; García-Díaz et al. 2015; Tingley et al. 2016) or studies from the native range that assess survivability during transit in hostile conditions, e.g. ship ballast water (Gollasch et al. 2000). With no likely single predictor of invasion risk, we propose that combining functional responses with proxies for numerical responses, plus propagule pressure, offers an effective three-pronged assessment that spans the invasion process.

Conclusion

Using our impact potential metric, the turtle warranting management priority is *Trachemys scripta scripta*. While uncertainty surrounds the ability and timeframe of all four turtles to adapt to more temperate climates, the potential for high relative clutch size, high feeding rate on a locally abundant prey, large body size and aggression to ward off potential competitors and predators, mean the likelihood of establishment and ecological impact of *T. s. scripta* is high. However, the widespread availability of *S. odoratus*, combined with a wide range of habitats, TSDII reproduction and the same population destabilising Type II functional response as *T. s. scripta*, mean the Relative

Invasion Risk (RIR) triplots highlight this as a species that would otherwise have been overlooked solely on the basis of Comparative Functional Response (CFR) and Relative Impact Potential (RIP) studies.

With the pet trade likely to continue to be the main driver of any turtle species arriving, either by release or escape, knowing the species being imported into local pet shops and being sold by owners, is of vital importance. For that reason, the RIR triplots, which combine IP data with a measure of propagule pressure (i.e. PPP), offer an informative way of prioritising potential invasive species for management interventions. Going forward, there is vital need for regular surveys and for assessing the potential impact and risks of newly arrived specimens. With some turtle species encountered in both PPP surveys that were not investigated in this study, what we have provided is an avenue for further research and a starting point for the compilation of a user-friendly database of potential pet shop invaders to help decision-makers worldwide to assess IAS impact and invasion risk. More broadly, in terms of future research and management directions, there is a need for compilation of data on alien species functional responses, that is, existing and new data similar to those collated for biocontrol agents. We also need better estimates of numerical responses, as this latter measure is the gold standard for providing the total response and hence impact of invaders (see Dick et al. 2017b). Further, where our numerical response proxies are used in metrics, more ground-truthing of their predictive capacities is required, although this may only come with new invasions and monitoring of their actual impacts. Propagule measures also need more careful and imaginative derivations and examined for actual performance against real invasions.

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Supplementary material 1

Table S1. The locations of the 20 pet shops surveyed across Northern Ireland

Authors: James W.E. Dickey, Ross N. Cuthbert, Michael Rea, Ciaran Lavery, Kate Crane, Josie South, Elizabetha Briski, Xuexiu Chang, Neil E. Coughlan, Hugh J. MacIsaac, Anthony Ricciardi, Gillian E. Riddell, Meng Xu, Jaimie T.A. Dick

Data type: occurrence

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Link: <https://doi.org/10.3897/neobiota.40.28519.suppl1>

Supplementary material 2

Table S2. Summary of the GB online survey outlining which of the four species of turtle was being sold

Authors: James W.E. Dickey, Ross N. Cuthbert, Michael Rea, Ciaran Lavery, Kate Crane, Josie South, Elizabetha Briski, Xuexiu Chang, Neil E. Coughlan, Hugh J. MacIsaac, Anthony Ricciardi, Gillian E. Riddell, Meng Xu, Jaimie T.A. Dick

Data type: species data

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Supplementary material 3

R Script Biplot Creation

Authors: James W.E. Dickey, Ross N. Cuthbert, Michael Rea, Ciaran Lavery, Kate Crane, Josie South, Elizabetha Briski, Xuexiu Chang, Neil E. Coughlan, Hugh J. MacIsaac, Anthony Ricciardi, Gillian E. Riddell, Meng Xu, Jaimie T.A. Dick

Data type: statistical data

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Supplementary material 4

R Script Triplot Creation

Authors: James W.E. Dickey, Ross N. Cuthbert, Michael Rea, Ciaran Lavery, Kate Crane, Josie South, Elizabeta Briski, Xuexiu Chang, Neil E. Coughlan, Hugh J. MacIsaac, Anthony Ricciardi, Gillian E. Riddell, Meng Xu, Jaimie T.A. Dick

Data type: statistical data

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Supplementary material 5

Outlining RIP and RIR data

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Data type: statistical data

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Forecasting the global extent of invasion of the cereal pest *Spodoptera frugiperda*, the fall armyworm

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Abstract

Fall armyworm, *Spodoptera frugiperda*, is a crop pest native to the Americas, which has invaded and spread throughout sub-Saharan Africa within two years. Recent estimates of 20–50% maize yield loss in Africa suggest severe impact on livelihoods. Fall armyworm is still infilling its potential range in Africa and could spread to other continents. In order to understand fall armyworm's year-round, global, potential distribution, we used evidence of the effects of temperature and precipitation on fall armyworm life-history, combined with data on native and African distributions to construct Species Distribution Models (SDMs). We also investigated the strength of trade and transportation pathways that could carry fall armyworm beyond Africa. Up till now, fall armyworm has only invaded areas that have a climate similar to the native distribution, validating the use of climatic SDMs. The strongest climatic limits on fall armyworm's year-round distribution are the coldest annual temperature and the amount of rain in the wet season. Much of sub-Saharan Africa can host year-round fall armyworm populations, but the likelihoods of colonising North Africa and seasonal migrations into Europe are hard to predict. South and Southeast Asia and Australia have climate conditions that would permit fall armyworm to invade. Current trade and transportation routes reveal Australia, China, India, Indonesia, Malaysia, Philippines and Thailand face high threat of fall armyworm invasions originating from Africa.

Keywords

Agriculture, biological invasion, climate envelope, crop pest, ecological niche model

Introduction

Fall armyworm, *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae) is native to the Americas. The moth lives year-round from as far south as La Pampa, Argentina, to as far north as southern Florida and Texas, USA and undergoes seasonal migrations as far north as Québec and Ontario (Figure 1). Fall armyworm caterpillars are major pests of cereals and forage grasses and are recorded as eating 186 plant species from 42 families (Casmuz Augusto 2010). Fall armyworm is one of the most serious pests of maize in the America. Yield losses can reach 40% in Honduras (Wyckhuys and O’Neil 2006) and 72% in Argentina (Murúa et al. 2006). In addition to maize, fall armyworm attacks many other economically important, e.g. rice, sugarcane, sorghum, beet, tomato, potato, cotton and pasture grasses (Abrahams et al. 2017; Day et al. 2017). Therefore fall armyworm could pose a risk to subsistence and cash crops in large parts of the world.

In January 2016, major outbreaks of armyworms were reported in South West Nigeria and Ghana and shortly after in Benin, Sao Tomé and Togo (International Institute of Tropical Agriculture 2016). Morphological and molecular analysis confirmed that the armyworms were *S. frugiperda* and not the native armyworms *S. exigua* or *exempta* (CGIAR 2016). As of 28 September 2017, 28 sub-Saharan African countries had confirmed the presence of fall armyworm, with nine more suspecting or awaiting confirmation of the species’ presence (Abrahams et al. 2017). Within these countries the fall armyworm is still spreading (Njeru 2017). The countries of the initial outbreaks (Ghana, Benin, Togo and Nigeria) have West Africa’s major air transportation hubs and have similar warm, moist climates to the regions from which many arriving flights originate (Chapman et al. 2017; Tatem 2009). As a result, this region is particularly likely to act as an epicentre for invasions in Africa (Early et al. 2016). Indeed, it is speculated that fall armyworm entered Africa as a stowaway on a passenger flight (Cock et al. 2017); unaided dispersal is considered unlikely because prevailing winds are generally from East to West. Molecular data from specimens in Togo indicate that fall armyworm in Africa originates from an area encompassing the eastern USA, Caribbean and Lesser Antilles (Nagoshi et al. 2017). The two known strains of the species, the so-called maize- and rice strains, overlap in the latter region and both strains have been found in Africa (Cock et al. 2017, Nagoshi et al. 2017). However, it is still unclear whether the invasion originated from single or multiple introductions. Differences in host plant and mating time between the strains (Hänniger et al. 2017) suggest it is unlikely that both strains would have been introduced separately. The rapid spread throughout Africa was possibly aided by intra-continental transportation links (Faulkner et al. 2017). However, the ability of adult fall armyworm moths to travel very long distances was probably the major factor. Adults can travel several hundred kilometres in a single night by flying to and maintaining an elevation of several hundred metres, at which height winds can transport them in a directional manner (Westbrook et al. 2016).

Fall armyworm’s year-round distribution is expected to be restricted to relatively warm and moist areas, as it cannot survive cold temperatures by entering diapause (Nagoshi et al. 2012). However, fall armyworm poses a threat outside its year-round range,

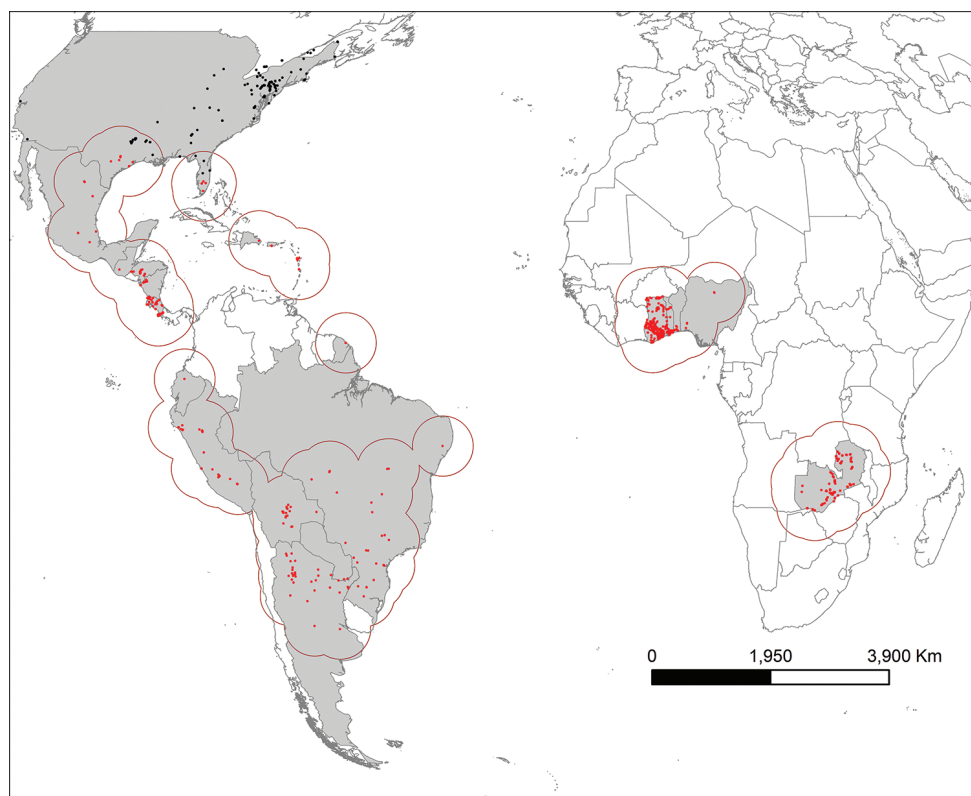


Figure 1. Fall armyworm distribution data. Red points are the complete set of presence locations used to make models. Black points in the USA are not part of the year-round native distribution and were not included in models. Grey areas are the geographically unrestricted background from which pseudo-absences could be drawn. Red lines indicate the geographically restricted background (500 km radius around presence locations) within which pseudo-absences could be drawn.

including in temperate regions, because it undergoes very long distance seasonal migrations. Between spring and autumn, three successive generations of fall armyworm travel 1700 km north from Texas and Florida to infest crops as far north as Québec and Ontario (Westbrook et al. 2016). Adults also appear to migrate several hundred kilometres over the sea (Westbrook et al. 2016). This means that North African countries could be within the reach of fall armyworm from sub-Saharan populations. If the species can survive year-round in North Africa, then seasonal migrations into Europe could also occur. This would pose a severe threat to agriculture in Europe, where the species is classed as a Quarantine Pest by the EU (Efsa Panel on Plant Health et al. 2017). Further afield, the fall armyworm's wide distribution in the Americas and Africa suggest that it could establish easily in East and Southeast Asia. Given increasing levels of trade and transportation between infested parts of Africa and the rest of the world (Chapman et al. 2017), it seems likely that fall armyworm could be unwittingly transported onwards to environmentally suitable regions.

As fall armyworm has huge potential to affect staple and economic crops globally, we urgently need information on the pest's potential distribution and environmental limitations. Such information would assist national and regional pest risk assessments and appropriate management strategies in several ways: by quantifying the agricultural areas within Africa that are at risk from year-round populations or seasonal migrations, by informing the likelihood of seasonal migrations outside Africa, and by classifying the likelihood of establishment if fall armyworm is transported into other parts of the world. This information would also help target awareness raising and monitoring for early detection. Early detection of infestations is extremely beneficial as chemical insecticides are only effective while the larvae are small (Bessin 2003). Early-stage larvae live inside the whorl of the developing plant and so are hard to detect with casual observation. Detecting fall armyworm in time to apply pesticide and avoid heavy crop losses means inspecting plants for eggs or larvae or setting pheromone traps for adults (Njeru 2017). Raising awareness amongst farmers and developing surveillance schemes is therefore a priority for managers (Njeru 2017). Knowing where outbreaks are likely to occur would encourage and inform these efforts.

Here, we first reviewed what is known of the environmental controls on the fall armyworm's life-cycle and herbivory, particularly on maize, the crop most economically important and threatened by the moth in Africa (Njeru 2017). We then quantified the species' environmental controls and potential distribution worldwide, using information on the native and invasive distributions to construct an ensemble SDM. SDMs find statistical correlations between species' distributions and environmental factors and ensembling results from multiple SDM types identifies areas that techniques agree are highly suitable for the species. We assessed the robustness of the SDM approach by asking whether fall armyworm has invaded parts of Africa, not predicted by a climatic SDM, i.e. undergone a 'niche shift' (Early and Sax 2014). The SDMs we constructed are based on annual environmental conditions and thus predict suitability for year-round populations of fall armyworm. Lastly, we use trade and transportation links to interpret the potential for the fall armyworm to spread beyond Africa via these pathways.

Methods

Effect of abiotic and host plant characteristics on life-cycle

To forecast a species' potential range, it is necessary to consider the environmental factors that are needed for the species to complete its life cycle. These factors could directly limit the target species' distribution and are often termed 'proximal' variables. Using these variables increase accuracy and biological realism of projections of species distributions following invasion (also termed 'transferability' (Petitpierre et al. 2017)). We reviewed the literature of field observations and experimental studies into fall armyworm to investigate the linkages between the environment and life cycle (Figure 2, Suppl. material 1: Table S1). The studies were conducted on different populations and

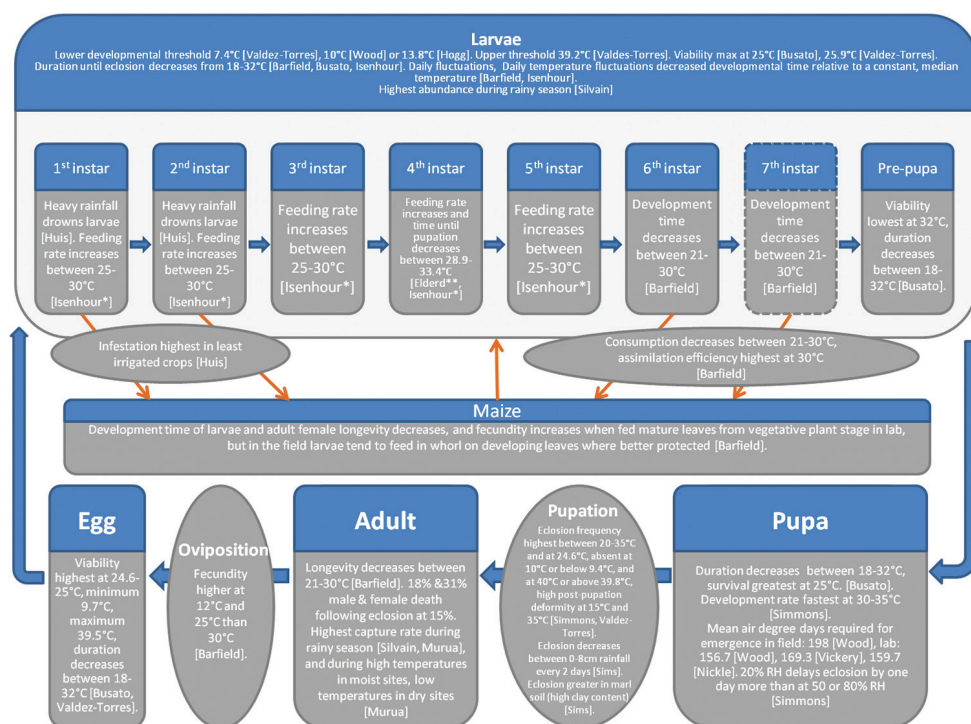


Figure 2. Empirically measured environmental effects on fall armyworm life cycle. Summary of data from literature of temperature, moisture, soil and host plant effects on fall armyworm survival and developmental time and observations of abundances in the field under different conditions and seasons. All studies were conducted with populations from the Americas. Rectangles are life stages, ovals are processes. Orange arrows represent effects of fall armyworm on maize or vice versa. The occurrence of a 7th instar is not universally reported. Only direct effects (measured or imputed) of the environment and host on fall armyworm were included. Unless otherwise noted, moths for experiments were reared on fresh maize or an artificial diet. RH is relative humidity. More information is given in Suppl. material 1: Table S1, Figure S5

the population's strain (which could affect physiology, see below) was rarely reported. Nonetheless, informative patterns emerged. We summarise the patterns below and in Figure 2, but full details and references are in Suppl. material 1: Table S1.

Environmental data

Based on the life-history and environmental requirements of fall armyworm, and in light of climatic conditions in the Americas and Africa, we selected the following climatic variables:

- SumWet, total amount of precipitation in wettest three months of year (intensity of rainy season, when most food available and population growth is fastest)

- LenWet, number of months when rain is greater than average (length of rainy season, when most food is available and population growth is fastest)
- SeasPpn, seasonality of precipitation (difference in rainfall between rainy and dry season)
- MinTemp, mean temperature of the coldest month of the year (the lowest limit for growth)

We also initially used GDD13.8, annual growing degree days above a lower development threshold of 13.8 °C (minimum temperature for survival). We selected 13.8 °C as the lower development threshold (Hogg et al. 1982), as this value is widely cited by other researchers. However, the correlation between MinTemp and GDD13.8 is 0.98. This degree of collinearity can cause inaccurate measurement of the relationship between the explanatory and response variables (Dormann et al. 2012). We removed GDD13.8, as MinTemp has the more intuitive link with species distributions and a clear temperature threshold for fall armyworm survival is widely reported (Suppl. material 1: Table S1). Indeed, fall armyworm populations in west Argentina occur in areas with substantially fewer growing degree days than the populations in the USA. This suggests that the cold range margin is more likely to be set by MinTemp than GDD. No other environmental variables had a collinearity greater than 0.7, which is considered an acceptable threshold (Dormann et al. 2012). There is considerable variation in the rainy season between America and other parts of the world, particularly Africa (Leff et al. 2004). The precipitation variables were therefore chosen to accommodate variation in the timing and length of the rainy season or even multiple rainy seasons (e.g. West vs. East Africa). Climatic variables were calculated from monthly averages for the period 1961–1990, derived from the climatic research unit (CRU) dataset at 10 arc-minute resolution (New et al. 2002).

In addition to climatic variables, we also used ‘Forest’, the proportion of each 10 arc-minute grid-cell that is covered by trees. This is because fall armyworm is only reported from agricultural areas, though there may be many areas covered by forest that are climatically suitable for the species, but from which it is not reported or is absent due to a lack of host plant. We therefore expected a high forest cover to indicate environmental unsuitability. Without the forest variable, climate conditions alone would have been less able to discriminate between suitable and unsuitable locations. We used forest rather than crop or pasture land as forest is relatively easier to delineate than grassland using satellite data. Forest cover was drawn from the European Space Agency’s Global Land Cover 2000 project at 1 km (<https://www.esa-landcover-cci.org/>).

Distribution data

Presence records for the Americas were obtained from three sources. 1) Global Biodiversity Information Facility (www.gbif.org) in November 2016. Records that did not have coordinates but did have location descriptions were georeferenced with accuracy equal to the climatic grid data. 2) Review of literature on Fall Armyworm in the region.

3) Consultation between CABI and local experts in several countries. In the southern USA, occurrences south of 27 degrees in Florida and south of 31 degrees in Texas were considered to be year-round populations and were included as presence data points (Westbrook et al. 2016). Other USA populations were not included as they represent seasonal migratory populations. In total, 876 presence locations were found. Data and sources for the Americas that can be shared publicly are available in Suppl. material 2: Table S2. Distribution data for Africa were obtained from four sources. 1) A survey of farming households in Ghana and Zambia, conducted in July 2017 (Abrahams et al. 2017). The countries were stratified into geographic regions, within which survey locations were chosen randomly. Surveys yielded 466 incidences of farming households observing symptoms or larvae of fall armyworm in their fields. 2) Published literature (Goergen et al. 2016; Nagoshi et al. 2017). 3) Infestations of fall armyworm reported to CABI's Plantwise clinics in Ghana and Zambia from July 2016–June 2017. 4) Seven pheromone traps in Ghana managed by the USAID Agricultural Development and Value Chain Enhancement (ADVANCE) project, from April 2017–July 2017.

Distribution data were filtered so that only one presence was recorded in each climatic grid-cell, resulting in 240 presences in Africa and 167 presences in the Americas. Due to the recent dedicated searches, the African distribution was better sampled than the American distribution. The difference in sampling intensity between the two continents led to concerns that SDMs might be over-fitted to the well-studied locations in Ghana and Zambia. This would underestimate the suitability of areas outside Ghana and Zambia, particularly areas that are environmentally similar to the native range, but different to the Ghanaian and Zambian range. We therefore sub-sampled several proportions of the African distribution (5, 10, 20, 30, 50 and 70%) and used four sub-samples at each proportion to construct alternative SDMs.

In order to select pseudo-absences, we used two approaches to delimit the geographic background in the Americas and Africa to which fall armyworm could reasonably be expected to disperse without human assistance (Figure 2, VanDerWal et al. 2009). First, we used all countries in America and Africa in which fall armyworm records were available. American countries were excluded from the backgrounds if they did not have records of fall armyworm but (i) fall armyworm is known to be present (determined using CABI's Crop Protection Compendium, <https://www.cabi.org/cpc/about/> and internet searches) or (ii) if the country is surrounded by countries in which fall armyworm is recorded. This exclusion avoided the inclusion of countries in the background where the species is present but had not been sampled, reducing the probability of 'false absences'. Second, we investigated the impacts of restricting the geographic background to the region within 500 km of presence points (Figure 1). Specifying an upper distance can help prevent models from contrasting completely different climate conditions, e.g. temperate vs. tropical (VanDerWal et al. 2009). This contrast would only yield the information that fall armyworm can live in the tropics all year round. For both approaches, pseudo-absences were randomly placed in climatic grid-cells within the background region, but outside occupied grid-cells. The placement of pseudo-absences was repeated 20 times for each sub-sample. In each distribu-

tion dataset, the number of pseudo-absences was the same as the number of presences used (i.e. prevalence was always 0.5).

In total, we ran models with 488 datasets: six different levels of sub-sampling of African presences from the entire background (5, 10, 20, 30, 50 and 70%) each with 20 repetitions of sub-sampling, one dataset of all presences using the entire background, and one dataset with the geographically restricted background and for each of which we randomly sampled pseudo-absences four times.

Species distribution modelling

In order to estimate parameter values for the environmental variables, and to predict the potential year-round distribution of fall armyworm, we created an ensemble SDM (Araújo and New 2007). The ensemble included eight modelling techniques: artificial neural networks (ANN), classification tree analysis (CTA), flexible discriminant analysis (FDA), generalised additive models (GAM), generalised linear models (GLM), multivariate adaptive regression splines (MARS), random forest (RF) and surface range envelope (SRE, note this does not use pseudo-absence data in model calibration but does in validation). Analyses were undertaken in R (R Core Team 2016) using the biomod2 package (Thuiller et al. 2014) and default SDM settings.

We used internal validation to evaluate SDM accuracy, splitting each of the 488 distribution datasets randomly so that 70% of the presence and pseudo-absence points were used to calibrate the models. These models were used to predict suitability at the 30% remaining validation distribution data points. The Area under the Receiver Operating Curve (AUC) and True Skill Statistic (TSS) were used to judge how accurately the models predicted the validation data (Lawson et al. 2014).

For each of the distribution datasets, we constructed an ensemble forecast for the global terrestrial surface. Ensembles were made using models (from the 488 distribution datasets) for which validation TSS ≥ 0.4 . Models with TSS ≥ 0.4 are considered to have ‘moderate’ performance (greater than ‘fair’, but less than ‘substantial’ (Landis and Koch 1977)). However, we used all presence and pseudo-absence points in the given dataset to construct the final models to be included in the ensemble (i.e. not just the 70% of the data used in calibration). This was to ensure that, when a combination of dataset and technique yielded moderate accuracy, all of the data in that dataset were then used to maximise the information in the final model. In order to be confident that TSS and AUCs of the internally validated models reflected the accuracy of the full models used to project distributions, we calculated the Spearman’s correlation between global projections from internally validated and full models. To construct ensembles, the selected models were rescaled so that projections were on the same numerical scale and the mean suitability predicted by all retained models was calculated, weighted by the accuracy (TSS) of each model. This method has been shown to be the most accurate of the ‘traditional’ ensembling methods that could be applied to these data (Gritti et al. 2013).

In order to investigate the effect of biased recorder effort and geographic background on environmental suitability, we compared the agreement of the global ensemble projections made using each distribution dataset by using Cohen's Kappa and balanced accuracy (Brodersen et al. 2010). For the latter, we binned projected suitabilities into 20 percentile bins and calculated how well the projections from one dataset classified the projections from another dataset.

In order to determine whether the environment in the geographic region from which distribution data were drawn is representative of the entire global terrestrial surface, we calculated the Multivariate Environmental Similarity Surface (Elith et al. 2010; Hijmans et al. 2012). If there are environmental conditions somewhere in the world that have "no analogue" with environmental conditions in the American and African backgrounds, SDM projections into these regions would be extrapolations, with added uncertainty.

The importance of environmental variables for fall armyworm's range was calculated using all of the distribution data in a given dataset and using all models, regardless of TSS score. For any given environmental variable, that variable was randomised, an SDM was made with the shuffled dataset and the Pearson's correlation (r) calculated between the SDMs with original and shuffled data. Importance is calculated as $1-r$, so a value 0 indicates the variable has no influence on the SDM.

Has the fall armyworm invaded where we expect it to, based on the native distribution in the Americas?

To answer this, we calculated the niche expansion between the Americas and Africa, using the methodology developed by Broennimann et al. (2012). The environment (climate and forest cover) in the two regions is decomposed into the most important trends using a Principal Components Analysis (PCA). We used all distribution data from the native year-round range and from the studied African range in Figure 1 (i.e. there was no sub-sampling). We then divided this environmental space into a grid of 100×100 cells. We measured the density of species occurrences for each combination of environmental conditions in each grid-cell of the environmental space using a kernel smoother function to correct for sampling bias and environmental availability and to ensure that the results were independent of the grid resolution. These analyses were done using ecospat package (Di Cola et al. 2017) in R v3.4.1 (R Development Core Team 2017). We used these gridded data to calculate how much of the African niche remained within the native niche ('niche stability'). Niche stability is the proportion of the densities in the colonised range that overlaps with the native range.

Transportation beyond Africa

In order to illustrate the potential for fall armyworm to spread from Africa to other parts of the world, we first identified the countries most likely to act as sources for fall armyworm and the countries most vulnerable to fall armyworm establishment, as

those with $> 33660 \text{ km}^2$ of suitable climate (i.e. 100×10 arc-minute grid-cells with climate suitability > 0.5). This resulted in 64 countries being identified as sources or vulnerable. We then examined two major pathways for invertebrate introduction: trade and passenger air travel. Trade is one of the main drivers of plant pest introduction globally (Chapman et al. 2017). We used values of all traded goods, as the propensity of fall armyworm to be transported with particular commodity types is not yet known, and all trade provides a reasonable estimate of introduction likelihood for a range of species (Seebens et al. 2015). We obtained United Nations data on total exports from sub-Saharan African countries to all countries for the period 2012–2016 (2017 data appeared to be too incomplete to use). Data were obtained from the UN Comtrade database (<https://comtrade.un.org/>). We considered the trade routes most likely to transport fall armyworm as those with a total trade volume $> 500,000,000$ USD during the reporting period (the top 5% of trade routes from source to vulnerable countries).

Passenger air travel is suggested to be the route by which fall armyworm was first introduced to Africa and is thought to be important in insect introductions (Tatem and Hay 2007). Of 725,000 interceptions of plant pests (largely insects) in the US, 62% of intercepted pests were associated with baggage (McCullough et al. 2006). We used data on the number of passengers in 2013 whose embarkation point is in a sub-Saharan African country and whose final destination is outside sub-Saharan Africa. Data were obtained from the VBD-Air tool (Huang et al. 2012). We considered the country to country air travel routes most likely to transport fall armyworm as those that carry > 10000 passengers during the reporting period (the top 13% of air travel routes from source to vulnerable countries). We then mapped the trade and air travel routes from source countries in sub-Saharan Africa to vulnerable countries worldwide.

Results

Effect of abiotic and host plant characteristics on life-cycle

The most commonly studied relationship between life-history stage and environment is the effect of air temperature on larval and pupal survival and development rates. The minimum temperature for development was reported between 8.7°C and 13.8°C (Busato et al. 2005; Hogg et al. 1982; Valdez-Torres et al. 2012; Wood et al. 1979). Several studies found evidence that the developmental time of egg, larval, pre-pupal and pupal stages decreases with temperature up until $32\text{--}33.5^\circ\text{C}$ (or even 35°C) (Barfield and Ashley 1987; Busato et al. 2005; Elderd and Reilly 2014; Hogg et al. 1982; J. Isenhour et al. 1985; Simmons 1993). However survival of these stages is greatest around 25°C (between 20 and 32°C), and 35°C appears to be an upper limit on survival (Barfield and Ashley 1987; Busato et al. 2005; Simmons 1993; Valdez-Torres et al. 2012). Fecundity and adult longevity is greatest between 21 and 25°C (Barfield and Ashley 1987). Constant temperatures do not represent real conditions in the field and studying the effects of fluctuations can be informative. When median temperatures are between 15 and 25°C ,

daily fluctuations above and below these temperatures increase pupal and larval development rates and decrease adult deformity (Barfield and Ashley 1987; Simmons 1993).

The importance of moisture and precipitation is complex. Precipitation and irrigation have a direct negative effect on larval and pupal survival. Heavy rainfall fills the maize whorl with water, in which larvae float, until it overflows and the larvae are spilled out or drown (a process which is helped by wind gusts, A. van Huis 1981). Rainfall and irrigation are thought to trap moths and drown them in their pupation tunnels, with the effects being stronger in more friable soils, when rainfall can also cause the tunnels to collapse (Sims 2008). In fact, a local control measurement in Zambia involves spreading ashes in the funnel in order to exacerbate the effect of water (pers. comm. Patrick Kalama). Lack of moisture during pupal stages appears to have little direct effect on survival or development rates (Simmons 1993). However, indirect effects of moisture are likely more important for fall armyworm population sizes than direct effects. This is because abundance tends to peak during rainy seasons, particularly in drier sites, possibly because of increased host plant growth (Murúa et al. 2006; Silvain and Ti-A-Hing 1985). On the other hand, infestation rates are highest in maize deprived of irrigation for the longest, likely because plant moisture stress favours insect development (van Huis 1981).

Research on the effect of host plant on fall armyworm populations is limited to maize. There is evidence that the maize growth stage positively impacts development speeds (i.e. development is fastest for larvae eating mature leaves) (Barfield and Ashley 1987). This is unexpected, as leaf nutritional value typically declines with growth stage. It is unclear whether this finding is relevant to field populations, as larvae prefer to feed in whorls on developing leaves, presumably for protection (Chapman et al. 1999).

There are two genetically distinct fall armyworm 'strains', which specialise on maize and rice (Nagoshi et al. 2007). Some inter-strain mating can occur; rice strain females prefer to accept maize strain males, resulting in mixed populations, but maize strain females and rice strain males appear to be reproductively incompatible (Hardke et al. 2015). Both strains appear to be present in Africa (Cock et al. 2017; Nagoshi et al. 2017). The strains differ in the rates of larval development on the host plants, mating behaviour, use of food resources, resistance to insecticides and variation in susceptibility to plants expressing *Bacillus thuringiensis* (Bt) proteins (Hardke et al. 2015; Nagoshi et al. 2017). There is evidence for variation in the environmental tolerances of the two strains. Basal temperature was found to be 10.6 °C and 10.9 °C for two populations of the maize strain and 9.5 °C and 9.6 °C for two populations of the rice strain (though no statistical test was done, Busato et al. 2005) and seasonal abundance varies differently for the two strains in Florida (Nagoshi and Meagher 2004). There is therefore an argument for constructing separate SDMs for each strain, but the distributions and inter-breeding status of the two strains are not sufficiently known to do this and we therefore treat the strains as a single entity.

Has the fall armyworm invaded where we expect it to, based on the native distribution in the Americas?

All but 3% of the recorded current distribution in Ghana and Zambia is found in climate and forest conditions that match the native range, i.e. there is virtually no

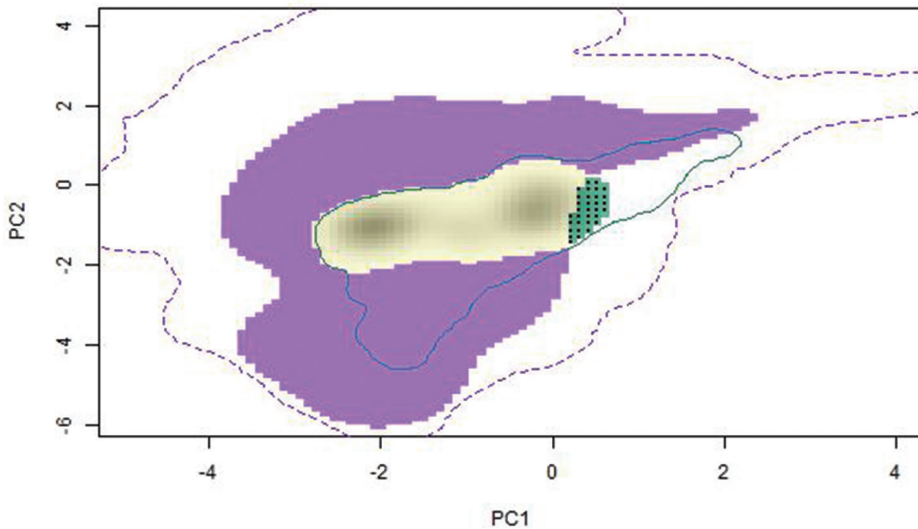


Figure 3. Similarity of environmental niches in the Americas and Africa. The outlines represent the environmental conditions available in the Americas (purple, solid line) and Ghana and Zambia (green, dashed). The larger purple shaded area represents the conditions the species occupies only in the Americas. The yellow shaded areas represent the conditions the species occupies in the studied African range that lie within the American environmental niche (niche stability). The green area with dots shows the part of the African range that is found in different environmental conditions to the native range (niche expansion). The shading under the yellow/green area is the density of the species' occurrence in the African range.

orange area in Figure 3. Fall armyworm therefore does not appear to have undergone niche shift during invasion.

SDM performance

Internal cross-validation indicated that TSS scores were 'moderate' and AUC scores were 'fair' (Table 1). These scores increased as more of the African distribution data were included in analyses. The Spearman correlations between global projections made using the validation data (70% of each distribution data set) and all data in each distribution dataset were ≥ 0.87 . This indicates that the TSS and AUC scores from internal validation reflect the accuracy of SDMs calculated with all data in each dataset.

Agreement between the ensemble projections resulting from sub-sampled and complete datasets was 'moderate' to 'substantial' (Cohen's kappa values Table 1, Suppl. material 1: Figure S1). Agreement increased with the percentage of the African data sub-sampled (Suppl. material 1: Figure S2). Ensemble projections from different datasets agreed most strongly in the areas that are least suitable, i.e. < 0.2 (Suppl. material 1: Figure S2). The proportion of grid-cells classified within the same suitability band ('balanced accu-

Table 1. Summary statistics for Species Distribution Models (SDMs). ‘Dataset’ indicates the percentage of the African distribution data that were sub-sampled. AUC and TSS indicate predictive accuracy. Mean ($\pm$ standard deviation) TSS and AUC values are averages calculated by internal cross-validation for all SDMs constructed with each dataset, excluding SDMs that were discarded in making the ensemble due to low predictive accuracy (TSS <0.4). TSS values between 0.4 and 0.5 are often considered ‘moderate’ (Landis and Koch 1977). AUC values between 0.7 and 0.8 are often considered ‘fair’. Spearman’s ρ is calculated between the global ensemble projections made using 70% (used for internal cross-validation) and 100% of the data and indicates whether the validation statistics can be considered representative of the final model. Cohen’s Kappa measures the agreement between the global ensemble forecast using 100% of the distribution data and the entire background and the named dataset. Kappa values of 0.4–0.6 are considered ‘moderate’, and 0.6–0.8 ‘substantial’ (Landis and Koch 1977).

Pseudo-absence restriction radius	Dataset	TSS	AUC	Spearman’s ρ	Cohen’s Kappa
None	5%	0.52 $\pm$ 0.06	0.79 $\pm$ 0.05	0.88 $\pm$ 0.12	0.49
None	10%	0.52 $\pm$ 0.07	0.80 $\pm$ 0.05	0.87 $\pm$ 0.15	0.50
None	20%	0.54 $\pm$ 0.09	0.80 $\pm$ 0.06	0.89 $\pm$ 0.09	0.57
None	30%	0.55 $\pm$ 0.06	0.80 $\pm$ 0.04	0.87 $\pm$ 0.12	0.59
None	50%	0.51 $\pm$ 0.07	0.79 $\pm$ 0.05	0.89 $\pm$ 0.11	0.75
None	70%	0.55 $\pm$ 0.07	0.91 $\pm$ 0.05	0.91 $\pm$ 0.09	0.76
None	100%	0.55 $\pm$ 0.07	0.81 $\pm$ 0.06	0.89 $\pm$ 0.08	NA
500 km	100%	0.48 $\pm$ 0.07	0.78 $\pm$ 0.04	0.79 $\pm$ 0.23	0.41

racy’) by different ensembles was never less than 0.6 when pseudo-absences were selected from the entire geographic background. Balanced accuracy and increased between ensembles constructed with similar degrees of sub-sampling (Suppl. material 1: Figure S2).

The dataset using 100% of the data and the entire geographic background gave SDMs that had the highest AUC and TSS scores (Table 1). There was very little difference in the shape or extent of the area in the native American region predicted to be suitable using different sub-samples of the distribution data (Suppl. material 1: Figure S1). This and the high degree of agreement in the global projections from SDMs using all and sub-sampled African data (Suppl. material 1: Figures S1, S2), suggest that SDMs using 100% of the data did not appear to be over-fit to the African distribution data. SDMs constructed using pseudo-absences drawn from a 500 m buffer around presence points (Figure 4) appeared to under-predict both the American and African distribution (Suppl. material 1: Figure S1) and had the lowest TSS and AUC scores (Table 1). We therefore saw no reason not to use predictions from SDMs using the complete distribution dataset and the entire geographic background to represent fall armyworm’s global potential distribution. These SDMs were used in the final ensemble global projection (Figure 4).

MinTemp was the most important environmental variable, followed by forest and SumWet (Figure 5). SeasPpn and LenWet were relatively unimportant. Fall armyworm was most commonly found in areas with very little forest cover, a minimum annual temperature of 18–26 °C and with 500–700 mm rainfall in the three wettest months (Suppl. material 1: Figure S3). The degree of sub-sampling did not affect variable importance. The range of the environmental conditions from which fall armyworm is recorded is shown in Suppl. material 1: Figure S3.

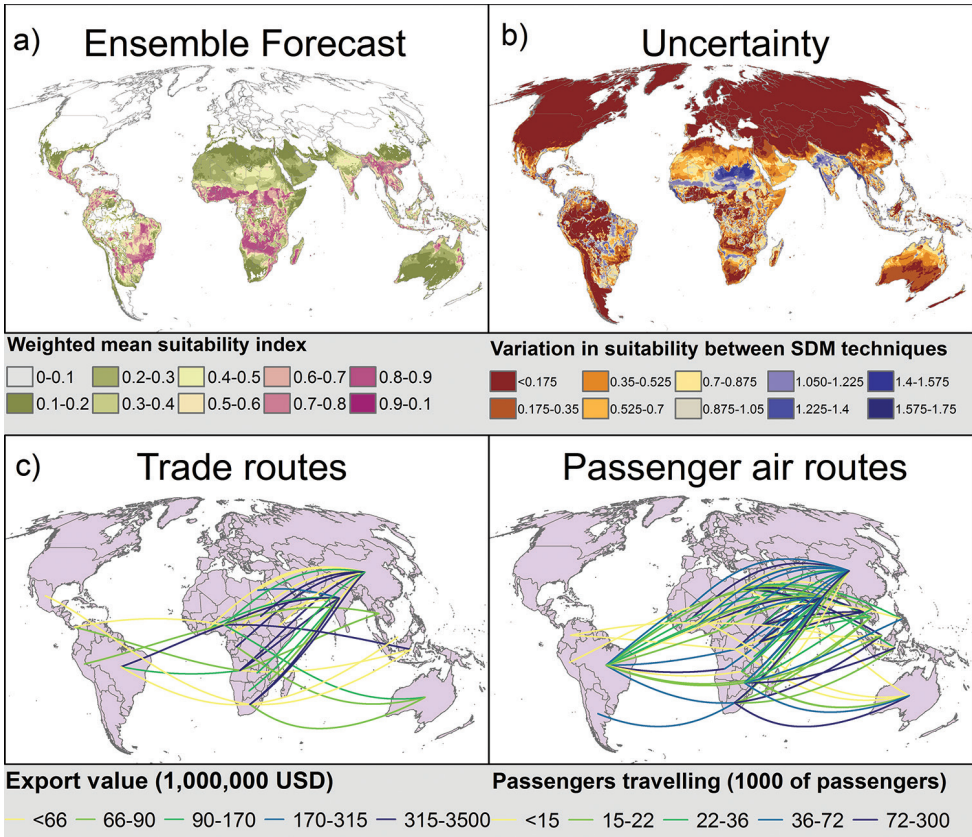


Figure 4. Global suitability for fall armyworm and likely invasion routes. **a** Potential global distribution of fall armyworm, as predicted by an ensemble of SDMs constructed using all distribution data and with four pseudo-absence datasets. SDMs were permitted into the ensemble if the TSS from internal cross-validation was ≥ 0.4 . The ensemble was calculated as the mean of projections from all permitted SDMs, each model weighted by the cross-validated TSS **b** uncertainty in projections, as calculated by the variation between all projections included in the ensemble **c** value of all exports from 2012–2016 from source sub-Saharan African countries climate to vulnerable countries outside sub-Saharan Africa. The top 5% of trading relationships between these countries are shown and the five colour categories represent 20% quantiles of export values **d** number of passengers in 2013 travelling from source sub-Saharan African countries with their final destination in vulnerable countries outside sub-Saharan Africa. The top 13% of travel routes between these countries are shown and the five colour categories represent 20% quantiles of passenger numbers.

MESS indicated very few areas in which environmental conditions had no analogue in the training region (Suppl. material 1: Figure S4).

Transportation beyond Africa

Countries vulnerable to fall armyworm (outside South America) that receive the greatest value of commodities exported from African fall armyworm source countries are

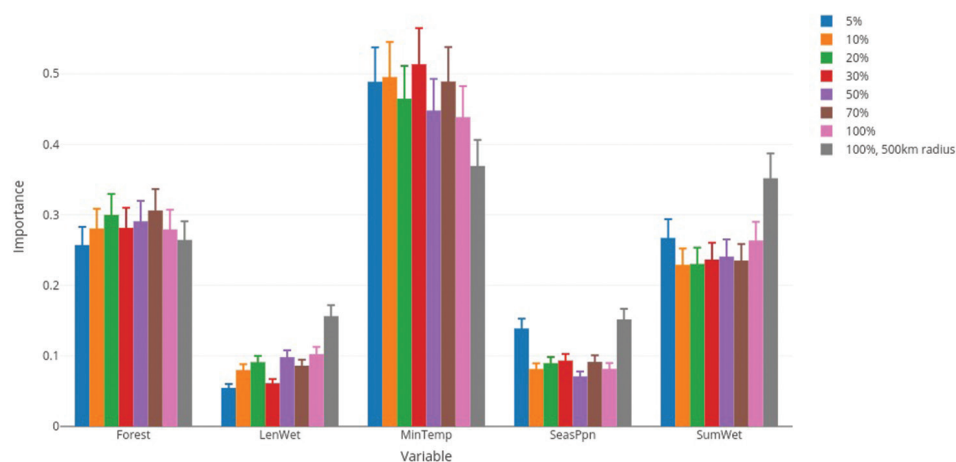


Figure 5. Importance of variables for Species Distribution Models (SDMs) of fall armyworm in the Americas and Africa. Colour codes indicate the percentage of the African distribution that was sub-sampled or the pseudo-absence selection background. Error bars are standard deviations of the results across all SDM techniques and distribution datasets.

China, India Indonesia and, to a lesser extent, Australia and Thailand. Countries vulnerable to fall armyworm (outside South America) that receive the greatest number of passengers embarking from African source countries are Australia, China, India, Indonesia, Malaysia and the Philippines. These countries are likely to be the most imminently threatened by fall armyworm invasion.

Discussion

SDM results were encouragingly accurate and indicated that much of sub-Saharan Africa is highly suitable year-round for fall armyworm, from the Saharan belt to South Africa. Within this region, much of Congo, DRC, Gabon and Cameroon have low suitability (though uncertainty is high in some of these areas). Low suitability in these countries is likely because of extensive forest cover. However, this does not mean that pockets of suitable habitat in those countries will not be severely affected, given the ability of fall armyworm to travel long distances (see below for further discussion of forested areas).

Much of Northwest and Northeast Africa has low suitability (<40% probability of occurrence, Figure 4), so might not host year-round populations of fall armyworm. However, Sudan's and Egypt's Nile Valley may be suitable during wet parts of the year and is adjacent to fall armyworm's likely year-round range in South Sudan and Ethiopia. Fall armyworm's 1700 km annual migration in North America suggests a similar migration could be possible into the Nile Valley, which could threaten maize and cotton production. Indeed, migrating fall armyworm is a severe pest of cotton in the USA (Hardke et al. 2015). Simulations of fall armyworm dispersal from the Khartoum area of Sudan and the Addis Ababa area of Ethiopia confirm this as a strong possibility (Heinrichs et al. 2018).

In currently un-invaded portions of Africa, there are pockets of high suitability in Morocco's productive agricultural regions, as well as the Libyan coast. Transportation to North Africa (countries with part of their land mass north of the Sahara) via trade or air transportation routes from sub-Saharan Africa is less likely than transportation outside Africa (Suppl. material 1: Figure S6). The suitable areas in Morocco are 2,500 km straight-line distance from the year-round distribution. This is far beyond the distance travelled by individuals from a single fall armyworm population in North America and so colonisation directly from the year-round distribution may be unlikely. However, some Lepidoptera are thought to migrate across the Sahara annually (Stefanescu et al. 2016). If fall armyworm were to establish in Morocco, seasonal migrations into Europe would be highly likely. There are pockets of climate suitable for year-round populations (i.e. grid-cells with a suitability value of ≥ 0.5) in south and northeast Iberia, Italy and Greece.

Low-suitability areas in sub-Saharan Africa may still experience infestation from migrating fall armyworm during some seasons. Nagoshi et al. (2007) suggested that considerable fall armyworm migration within Central and South America occurs in response to seasonal changes in rainfall, temperature and agricultural plantings. This is supported by the notable genetic mixing amongst populations as widely dispersed as Argentina, Mexico and Mississippi (Clark et al. 2007). Migration within Africa would make it very difficult to control fall armyworm outbreaks by managing any single location. Instead management would have to be coordinated across regions and country borders.

Research into seasonal migration and population dynamics within sub-Saharan Africa is clearly needed. Understanding the potential for annual migrations both within and beyond the year-round range requires forecasts of the speed, direction and heights of prevailing wind during periods when fall armyworm populations are large. We also need to know the migration capacity of African fall armyworm populations. The propensity of individuals to migrate and the length of time for which adults can fly varies within populations, often genetically (Roff and Fairbairn 2007). Migration capacity in Africa may differ from that in the putative native range, due to founder effects and selection during introduction. Using flight mills (Minter et al. 2018), Mark Release Recapture and population genetics could elucidate migration capacity. A cellular automata approach could be useful for modelling the spread of seasonal outbreaks (Garcia and Godoy 2017).

Much of South and Southeast Asia and areas of Australia are highly suitable for fall armyworm year-round. Natural dispersal towards this region is considered unlikely, as the distance is over 2000 km, further than fall armyworm is recorded to have travelled in the Americas. Nonetheless, the southwest monsoon blows from Africa to India beginning in June and is a possible route by which fall armyworm adults could arrive in India by their own dispersal. There are important invasion routes from Africa into South and Southeast Asia and Australia (Figure 4). Arrival via imported commodities or passenger air travel is most likely where entry ports are found in environmentally suitable locations for a given pest (Tatem and Hay 2007). Targeted screening and rapid response mechanisms could help reduce the likelihood of arrival and establishment in these locations. However, management efforts should not be confined to individual countries. There are large, spatially cohesive areas of environmentally suitable areas

throughout Asia and Australia (Figure 4a). The rapid spread in Africa suggests that, if fall armyworm reaches one location in Asia or Australia, it could spread throughout the entire region using its own dispersal mechanisms, rather than simply establishing near to the arrival point. Thus, if fall armyworm arrives anywhere in Asia or Australia, rapid cross-border communication and collaboration will be key to effective management.

As conditions outside the predicted year-round range (for example, Europe) might be suitable in certain seasons, improved predictions of seasonal suitability could be achieved with demographic modelling of data from lab or field trials or from statistical modelling (e.g. Tonnang et al. 2011). If demonstrated to be robust, demographic predictions could identify areas where crops eaten by fall armyworm are grown during seasons when migration could occur.

The results of Species Distribution Modelling were encouragingly accurate. AUC values from cross-validation were well within the range usually considered acceptable for SDM studies of invertebrates (Kharouba et al. 2013). This is encouraging given the somewhat uneven recording effort, the likelihood that fall armyworm is under-recorded in the Americas, and the large area for which projections were made. SDM projections were consistent across sub-sampled data. Indeed, areas in Colombia, Panama, Venezuela and Brazil known to harbour fall armyworm, but from which no or few presences were recorded, were predicted to be environmentally suitable (Figure 4). In addition to Ghana and Zambia, fall armyworm's distribution has been well characterised in South Africa. These data were not available to include in models, but visual inspection demonstrates that SDMs seem to predict the extent of fall armyworm's distribution in South Africa as reported in May 2017 (Erasmus 2017). Moreover, the predictions are broadly similar to those obtained from CLIMEX modelling (Du Plessis et al. June 2018). Projections from ensembles using differing data sub-samples did not lead to substantially lower suitability or greatly differing geographic patterns of suitability (Suppl. material 1: Figures S1, S2). This indicates that the intensive surveying in Ghana and Zambia has not caused over-fitting to environmental conditions in those countries.

Forest, MinTemp (coldest annual temperature) and SumWet (rainfall during the wettest three months) were consistently identified as the environmental variables that most affected fall armyworm's distribution. The importance of MinTemp supports the existence of a hard polewards geographical boundary, caused by one or more months where temperature drops below a threshold. This suggests that climate warming could expand the potential range of fall armyworm. SumWet was consistently more important than LenWet (rainy season length) or SeasPpn (the contrast between the rainy and dry seasons). In order to understand if this is due to indirect (i.e. through host plant growth) or direct effects, one could use structural equation modelling incorporating the yield of key host plants, or incorporate life-history parameters from Suppl. material 1: Table S1 into demographic models. The importance of 'Forest' is likely because it indicates the availability of crops on which fall armyworm feeds. This could also suggest that few people have looked for fall armyworm outside of areas with extensive crop coverage. It would be useful to study fall armyworm's survival in forested habitat and in small cropped areas

surrounded by forest. This would inform models of invasion into Congo, DRC, Gabon, and Cameroon, where low projected suitability is likely caused by high forest cover.

Rapid evolution of climate tolerances can occur in pest insects following invasion, i.e. a ‘niche shift’ (Hill et al. 2013; Hill et al. 2017). Evolutionary niche shifts would compromise invasion forecasts using any modelling technique relying on data from native populations. This includes SDMs (Early and Sax 2014), CLIMEX (Sutherst et al. 2004) and physiological and demographic approaches such as Insect Life Cycle Modeler (Tonnang et al. 2011). In addition to evolution, niche shifts can also occur during invasion due to species’ native distributions not occupying all environmentally suitable locations. However, non-evolutionary niche shifts are uncommon in widespread agricultural pests such as fall armyworm (Early and Sax 2014). In any case, niche shift analysis finds that rapid evolution of climate tolerances does not seem to have occurred for the fall armyworm (95% of the studied naturalised range display niche stability, Figure 3). It therefore appears that we can be confident in the accuracy of range forecasts that utilise native distribution data. However, there is still a significant part of the niche unoccupied in Ghana and Zambia that is suitable for the species based on the native range distribution. Thus, it is likely that the species will continue its rapid infilling of its potential African range (Day et al. 2017).

It is interesting to note that fall armyworm was not high on a recent list of pest species likely to invade West Africa (in the lower 50th percentile for Ghana, Nigeria and Togo (Paini et al. 2016, pers. comm. Paini). This list was constructed using a Self-Organising Map (SOM) approach. SOM calculates the relative likelihood a target pest species will establish in a region based on whether pests whose range overlaps the target species have also invaded there. The low establishment index calculated for fall armyworm is likely because few pest species have previously jumped from the Americas to Africa, which in turn is presumably because of historically low trade between the two continents (Cock et al. 2017; Seebens et al. 2015). While the SOM approach is highly valuable, rapidly changing global trade and transportation patterns open invasion routes that pest species rarely travelled in the past (Early et al. 2016; Seebens et al. 2015). Therefore, there may be many other inter-continental pest invasions that are hard to predict.

Very little research has been done into differing climate tolerances between maize and rice strains and there is insufficient information on their respective distributions to apply SDMs to each strain (see Methods). Slight differences in basal temperatures of the two strains result in approximately one more generation of the rice strain per year at the optimum temperature of 25 °C, i.e. 12 generations (Busato et al. 2005). The two strains appear to have substantially overlapping ranges, so any difference in tolerances is likely not to affect the geographic range greatly, but could affect abundance and impact. The African maize strain population appears to have passed through a genetic bottleneck (Abrahams et al. 2017). The population may thus have slightly more restricted climate tolerances than the species as a whole and environmental suitability worldwide may be overestimated. However, fall armyworm’s widely observed distribution in Africa suggests any overestimation is slight. The predominance of the maize strain in Africa may influence the establishment of

fall armyworm from Africa in environmentally suitable parts of Asia, where rice is much more widely grown than maize.

Diet can affect temperature tolerances, and indeed the temperature threshold for development was several degrees lower when fall armyworms were fed leaves from early vegetative maize plants than when fed leaves from late vegetative or reproductive plants (Barfield and Ashley 1987) (Suppl. material 1: Table S1). Environmental conditions can alter the impacts of biopesticides and infection rates of diseases and natural enemies that control pests, including in fall armyworm (Elder and Reilly 2014; Murúa et al. 2006; Tonnang et al. 2017). Predictions of range, abundance, impacts and the outcomes of Integrated Pest Management strategies would therefore benefit from a better understanding of the relationship between strains, diet, pesticide effectiveness and environmental limits on distributions. Given the encouragingly robust results of SDMs based on climate and land use variables, future work could extend statistical modelling to the relationship between environmental suitability and fall armyworm abundance and impact on crops. If data on the distribution of potential biocontrol agents could be obtained, their environmental suitability for these species could be also studied using SDMs.

Given the likely onward spread of fall armyworm, a united international response is clearly needed and is indeed emerging. In Africa, the Food and Agriculture Organization of the United Nations is coordinating responses to fall armyworm, providing support for early warning tools, farmer field schools on integrated pest management, and a food security risk assessment model. A research consortium uniting Africa and Asia has recently been launched. Led by CGIAR, the Fall Armyworm R4D consortium aims to develop integrated pest management solutions including host plant resistance, environmentally safer chemical pesticides, biological and cultural control methods and agronomic management.

Conclusion

The accuracy of SDM results and the similarity of the environments occupied in the native and invaded range support the robustness of the SDM approach. Temperature of the coldest month and the amount of rain during the rainy season are the most important climatic limits of fall armyworm's year-round distribution. Much of sub-Saharan Africa can host year-round fall armyworm populations and seasonal migrations are likely to take place along the Nile into Northeast Africa. The likelihood of seasonal migrations beyond this range seems to be low. South and Southeast Asia and Australia, are highly suitable for fall armyworm. Trade and passenger air travel routes indicate parts of this region into which African populations are particularly likely to be transported. There is therefore considerable potential for near global invasion and seasonal migration of fall armyworm. Vigilance is needed to monitor for the onward invasion of fall armyworm via potential migration routes into North Africa and South Asia and on some high-risk trade and air travel routes. Management decisions would be improved by further research on fall armyworm's seasonal migration and population dynamics and the environmental dependency of interactions with other species.

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Author contributions

RE conceived the study, collected data, performed analysis and drafted the paper. PG and SM contributed to the acquisition and interpretation of data for the project and revised the manuscript.

Data availability statement

Some distribution data from South America analysed during this study are included in the Supplementary Information files. This does not include data from Plantwise clinics in Bolivia, Honduras, Nicaragua and Peru, due to data sharing restrictions. Some other distribution data are available from CABI's Plantwise programme but restrictions apply to the availability of these data, which were used under licence for the current study and so are not publicly available. Data may be available from the authors upon reasonable request and with permission of Plantwise. All other data used are publicly available from the referenced data sources.

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Supplementary material 1

Supplementary material

Authors: Regan Early, Pablo González-Moreno, Sean T. Murphy, Roger Day

Data type: supplementary results

Explanation note: Table S1. Summary of evidence for fall armyworm developmental and population responses to the environment extracted from literature sources. Figure S1. Effect of different sub-sampling proportions and pseudo-absence selection diameters on model predictions (maps). Figure S2. Effect of different sub-sampling proportions and pseudo-absence selection diameters on Balanced Accuracy. Figure S3. Histograms of each environmental variable in 10 arc-minute grid-cells from which the fall armyworm is recorded. Figure S4. Multivariate Environmental Similarity Surface analysis. Figure S5. Empirically measured environmental effects on fall armyworm life cycle. Figure S6. Trade and passenger air transportation within Africa.

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Supplementary material 2

Table S2. Distribution data from the Americas

Authors: Regan Early, Pablo González-Moreno, Sean T. Murphy, Roger Day

Data type: occurrence

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Provenance of invaders has scale-dependent impacts in a changing wetland ecosystem

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Abstract

Exotic species are associated with a variety of impacts on biodiversity, but it is unclear whether impacts of exotic species differ from those of native species with similar growth forms or native species invading disturbed sites. We compared presence and abundance of native and exotic invaders with changes in wetland plant species diversity over a 28-year period by re-surveying 22 ponds to identify factors correlated with observed changes. We also compared communities found within dense patches of native and exotic emergent species with similar habits. Within patches, we found no categorical diversity differences between areas dominated by native or exotic emergent species. At the pond scale, the cover of the exotic grass *Phragmites australis* best predicted change in diversity and evenness over time, likely owing to its significant increase in coverage over the study period. These changes in diversity and evenness were strongest in younger, less successional-advanced ponds. Changes associated with cover of *P. australis* in these ponds were not consistent with expected diversity decreases, but instead with a dampening of diversity gains, such that the least-invaded ponds increased in diversity the most over the study period. There were more mixed effects on evenness, ranging from a reduction in evenness gains to actual losses of evenness in the ponds with highest invader cover. In this wetland complex, the habit, origin and invasiveness of species contribute to diversity responses in a scale- and context-dependent fashion. Future efforts to preserve diversity should focus on preventing the arrival and spread of invaders that have the potential to cover large areas at high densities, regardless of their origin. Future studies should also investigate more thoroughly how changes in diversity associated with species invasions are impacted by other ongoing ecosystem changes.

Keywords

wetland, invasion, exotic, *Phragmites*, *Typha*, scale, richness

Introduction

The impacts of exotic species on native species and plant communities are diverse. In many cases, exotic species have caused or contributed to extinction of native species (Ricciardi 2004; Sax and Gaines 2008; Pysek et al. 2017). However, in other cases, they benefit native species—for instance, by providing critical habitat or resources (Schlaepfer et al. 2011). In some cases, exotic species have led to local extirpation of natives and declines in local biodiversity (Vellend et al. 2013), whereas in other cases, no such losses in native diversity are apparent (Heard et al. 2012). These disparate and often contradictory impacts of exotic species have contributed to two ongoing debates relevant to both our ecological understanding of species invasions and their implications for conservation.

In the first debate, Davis et al. (2011) argued that the dichotomy between natives and exotics may be of little value and that species should instead be judged relative to their impacts. This point of view has been challenged (Simberloff et al. 2011; Simberloff et al. 2013). Indeed, if exotic species have some distinct advantage, such as escape from co-evolved enemies (Keane and Crawley 2002) or an intrinsic evolutionary fitness advantage (Fridley and Sax 2014), then they might be expected and, in some situations, have been shown to have disproportionately large impacts on native biota compared to native species (e.g. Paolucci et al. 2013). On the other hand, native species that are released from constraints by environmental change (e.g. climate change, severe disturbance) might also become ‘invasive’ and exert strong influences on ecological communities as their populations increase (Carey et al. 2012). Prominent examples of native invasive species include increases in the abundance of mountain bark beetle (*Dendroctonus ponderosae*) associated with climate change, which have led to the loss of native forests in western USA and increases in the abundance of white-tailed deer (*Odocoileus virginianus*) associated with a loss of predation pressure, which has negatively impacted native plant biodiversity in North American forests (Côté et al. 2004; Bentz et al. 2010). Likewise, eastern redcedar (*Juniperus virginiana*) is invading beyond its native range in central USA, where it is converting grasslands to forested habitat, with a corresponding loss of herbaceous plant diversity (Briggs et al. 2002), whereas fishes in western USA have often been moved small distances beyond their historic range boundaries, but nevertheless had large impacts on aquatic systems (Carey et al. 2012).

The second debate involves the expectation that invasions by exotic species typically lead to local biodiversity decline. While this expectation has been contested for some time (Sax and Gaines 2003) and many groups do show regional increases in richness following invasions, such as freshwater fish faunas (Toussaint et al. 2018), the debate, specifically on change in diversity at local scales, has intensified in the past few years (Vellend et al. 2013; Cardinale 2014; Dornelas et al. 2014a; Dornelas et al. 2014b; Vellend et al. 2017; Cardinale et al. 2018). The expectation of declines as a

consequence of environmental change - including invasions - has been a paradigm of recent ecological research. As a result, little attention has been placed on evaluation of diversity increases (e.g. Hector et al. 1999). However, while there are clearly documented declines in local-scale biodiversity following species invasions (Vellend et al. 2013), there are also well-documented counter-examples of no change or an increase in richness following invasions (Castilla et al. 2004; Sax et al. 2005). Meta-analyses of long-term change in ecological communities indicate that net increases in richness are at least as likely as net decreases in diversity at local scales (Vellend et al. 2013; Dornelas et al. 2014b; Elahi et al. 2015). However, the relevance and generality of these findings is debated (Cardinale 2014; Dornelas et al. 2014a; Vellend et al. 2017; Cardinale et al. 2018) and the role of invaders *per se* is difficult to determine, as too little of the data analysed to date explicitly examine the net impacts of invaders on species diversity (e.g. just 7 of the cases analysed in the meta-analysis by Vellend et al. 2013). This limitation is particularly acute within invaded systems that might simultaneously be experiencing succession or other environmental changes that impact species composition, where exotic invasive species may be 'passengers' rather than 'drivers' of change (MacDougall and Turkington 2005). Whether and when invaders might reduce diversity in a system that would otherwise be increasing in diversity is not well-understood.

While these two debates (species' provenances and invader-driven change in local diversity) have often been considered separately, they are, in fact, related. Intrinsic differences between native and exotic invaders could determine whether particular invasions are more likely to lead to decreases or increases in local-scale biodiversity. The answers to both debates are also likely to be influenced by the ways in which changes in biodiversity are measured (McGill et al. 2015) and whether species are considered native or exotic in a particular ecosystem. Here, we consider taxa to be exotic if their gene pool was introduced from a different continent; this typically applies to species but can also apply to genotypes that have been introduced from another continent and potentially hybrid species. We consider species to be native if they are known to occur historically within the region of study. Both native and exotic species can be considered invaders (with significant impacts on native ecosystems) if they have increased significantly in abundance over a period of interest (as we define here for our study system in Methods).

Determining whether native and exotic invaders have categorical differences in how they impact ecological communities and determining whether these impacts cause decreases in some measure of biodiversity is often difficult. The most straightforward comparisons will be possible when both native and exotic invaders have arrived or increased in abundance over similar time-frames, with relatively long periods of study. The Miller Woods section of the Indiana Dunes National Lakeshore is uniquely suited for a long-term comparison of the impacts of native and exotic invaders. This area has an extensive network of over 150 shallow ponds (Suppl. material 1: Figure S1), disturbed by fragmentation and hydrological change since the late 19th Century, that have been invaded by both native and exotic plant species (Wilcox and Simonin 1987; Jackson et al. 1988; Tonkovich 2003). A reconstruction of the plant community, using paleoecological techniques, shows which plant species were absent or rare before

human disturbance (Jackson et al. 1988) and an ecological survey conducted in 1982 (Wilcox and Simonin 1987) provides a baseline for comparing changes associated with invaders that have arrived or increased in abundance since that time.

In this study, we evaluated how native and exotic invader abundances are related to changes in vegetation richness, evenness and compositional similarity over 28 years. We examined these relationships for five invaders (two exotic, two native and one native-exotic hybrid) individually and in combination. We also considered whether other environmental variables such as pond age (and successional stage) can help explain the changes observed in these communities over the 28 years that have elapsed between surveys. Furthermore, we examined how one native-exotic hybrid, one exotic invader and two native dominants (one of which is an invader) are related to the richness and evenness of plant species at sub-pond spatial scales. These comparisons allowed us to consider the likelihood that the potential influence of native and exotic invaders differs within this wetland complex and to determine whether either set of invaders decreases biodiversity at local scales.

Methods

Study System

The over 150 shallow ponds in the Miller Woods section of the Indiana Dunes National Lakeshore formed in relatively discrete rows as Lake Michigan receded to its present level (Jackson et al. 1988). Pond age is thought to range from a few hundred years for those closest to the shore to > 3000 years for the oldest ponds (Futyma 1985; Jackson et al. 1988). The ponds are generally well-buffered with low nutrient concentrations, without large differences in water or sediment chemistry between young and old ponds (Wilcox and Simonin 1987). Ponds closest to the shoreline are irregularly shaped and are generally smaller, deeper and have less sediment than older ponds (Wilcox and Simonin 1987). Dunes around these ponds are large and hummocky and vegetated primarily by dune grasses and scattered cottonwood trees, *Populus deltoides*. Ponds further from the Lake Michigan shoreline are typically large and linear in shape. These ponds are situated in oak (*Quercus velutina*) woodlands, although pre-settlement woodlands also included pines (*Pinus strobus*, *P. banksiana*) (Jackson et al. 1988). Many ponds are fragments of historically larger ponds that were bisected by sand migration and powerline, railroad or road rights-of-way prior to initial vegetation surveys; some roads or railroads have been abandoned, but the causeways that alter pond hydrology remain in place.

Pond resurveys

We conducted resurveys of vascular plants and aquatic macrophytes in 22 ponds originally sampled in 1982 (Wilcox and Simonin 1987, Suppl. material 1: Figure S1), resur-

pling 12 in 2010 and 10 in 2011. In 2011, we also resampled five ponds sampled in 2010 to evaluate between-year consistency. As richness was highly correlated between years ($P < 0.05$, $R^2 = 0.80$), for ponds resampled in both years, we only report the 2010 data. In 1982, researchers placed four 1-m² quadrats randomly along five evenly spaced north-south transects that spanned the width of each surveyed pond. Transects were not permanently marked or mapped and pond size and shape had often changed, so we could not precisely relocate the original sample locations. In the resample, we placed 1-m² quadrats randomly along four to ten evenly spaced north-south transects, for a total of 20 to 145 1-m² samples in each pond, with larger sample sizes in larger ponds. In each quadrat, we recorded percent cover of all species, water depth and sediment type. Percent cover was estimated as total area covered when visualised from directly above the tallest plants, including cover above the water, within the water and just above the substrate surface. When the substrate surface in deep water was not visible due to plants in the water column or due to murky water, then we gently moved plants aside or waited for sediment to settle before taking measurements down to the deepest level visible. In locations with deeper submersed aquatic vegetation, we physically pulled samples to ensure we had not missed any species. Total percent cover values of quadrats could exceed 100% because of the multiple strata of plants (emergents, floating-leaved, submerged).

We subsampled 2010 and 2011 quadrats down to 20 quadrats per pond to provide equivalent sampling effort to the 1982 dataset for some analyses, including richness and evenness. A total of 20 quadrats were selected to best replicate the Wilcox and Simonin (1987) sampling layout, with 4–5 quadrats selected using a random number generator on each of 4–5 transects selected to span the length of the pond. To evaluate the impact of subsampling our data, we calculated sample-based rarefaction curves using all quadrats we sampled for each pond. We then calculated the correlation between subsampled richness and analytically estimated richness at 20 quadrats. Richness estimates were calculated in EstimateS v.8.0 (Colwell 2009). Subsampled and analytically estimated richness of 2010/2011 data were highly correlated, with an adjusted R^2 of 0.938 and the intercept was not significantly different from zero. Given the high correlation between sampling strategies within the resample period, we are confident the resample data adequately replicated the original sampling strategy.

We updated the names of taxa from the 1982 sample to reflect modern taxonomy. Species within some genera (e.g. *Persicaria*, *Nuphar*) had been split or joined in the intervening time, so we analysed those taxa at their lowest resolution. Other taxa contained species with variable morphology that were sampled in a vegetative state; those species could not be definitively identified, so we combined those species into morphotaxa.

Digitised GIS layers, created by the National Park Service in 2006, were used to calculate the area and perimeter of each pond. Average pond depth (cm) was calculated by averaging depths from all sampled quadrats. We designated ponds as ‘young’ (Wilcox and Simonin’s row 1 and 2, 300 to < 2,000 years old) or ‘old’ (rows 3–5, 2,000 to 3,000 years old), based on their ages and distance to shore (Futyma 1985; Wilcox and Simonin 1987; Jackson et al. 1988). Young ponds and old ponds clustered separately in the original vegetation survey (Wilcox and Simonin 1987) and we hypothesised that

plant communities between these groups may have changed distinctly over 28 years due to factors such as initial vegetation conditions or differential physical characteristics of the ponds. We used the ruler function in arcGIS 9.3 (ESRI 2010) on aerial photos to measure the fraction of pond perimeters comprising road or railroad rights-of-way, all of which were emplaced before 1982.

We used single classification G-tests and replicated tests for goodness-of-fit to identify taxa that were significantly increasing or decreasing in quadrat frequency of occurrence within and across ponds (Sokal and Rohlf 1995). The single-classification G-statistic tests for a change in frequency of occurrence of a particular species at a given pond. The G_{total} statistic for a species tests for changes in frequency in either direction across all ponds. The G_{pooled} statistic tests for overall net increases or decreases in frequency by combining data from all ponds. We classified species as “increasers” or “decreasers” if their changes were large enough and consistent enough to result in significant G_{total} and G_{pooled} test statistics (after the false discovery rate p -value correction for multiple hypothesis tests). Taxa were only investigated in this manner if they had greater than 1% frequency of occurrence (13 quadrats) in our study.

Species were classified as “Invaders” in our study if they both increased significantly in frequency of occurrence over the past 28 years across the wetland complex (Suppl. material 1: Table S1) and, for native species, also had their greatest long-term abundance (judged from macrofossil or pollen records spanning the last 3000 years) within the past 150 years (Jackson et al. 1988). This 150-year time period was chosen to reflect the significant changes European settlement had on the dunes landscape, when large shifts in community composition are visible in paleoecological records (Jackson et al. 1988). Using these criteria, five species were classified as invaders. *Typha* × *glauca* (hybrid cattail), a swarm of hybrids of native *Typha latifolia* and exotic *Typha angustifolia* (Freeland et al. 2013, but see Pederson et al. 2005), is an emergent taxon that has been abundant since the original survey was performed in the 1980s (Wilcox and Simonin 1987). The majority of the cattails present in the Upper Midwest, including Indiana Dunes, are *T.* × *glauca* hybrids (Travis et al. 2010). Historically, the native *Typha latifolia* was scarce before Euro-American settlement, increasing in abundance in the late 1800s (Jackson et al. 1988). *Phragmites australis* (common reed), probably a European genotype (Saltonstall 2002; Chun and Choi 2009), is an emergent grass that was rare in the 1982 surveys but expanded in the region between 1972 and 1990 (Tonkovich 2003). *Cephalanthus occidentalis* (buttonbush), an emergent native wetland shrub, was rare pre-settlement but increased substantially in the 20th Century, dominating some ponds today (Jackson et al. 1988; Tonkovich 2003). *Lythrum salicaria* (purple loosestrife), an emergent exotic dicot herb with plentiful seed production, was introduced to the Great Lakes in the mid-1800s but was absent in the 1982 survey. In the ensuing 30 years, it colonised the wetland complex and was very abundant by the early 2000s (Tonkovich 2003). It has been partially controlled locally by a beetle biocontrol agent (K. Amatangelo, pers. obs.). *Persicaria hydropiperoides* (swamp smartweed) is a native emergent dicot herb that was rare before Euro-American settlement and has become more abundant since the mid-late 19th Century (Jackson et al. 1988). Although there

were five other native taxa identified as ‘increasers’ in the past 28 years (Suppl. material 1: Table S1), these taxa were most abundant prior to 150 years ago based on paleo-ecological data, so they were not counted as ‘invaders’.

To evaluate whether provenance or habit predicted direction of change over the 28 years as evaluated by Gtests (increasers, decreaseers or no change), we performed tests for association using the Fisher Exact test with the Freeman-Halton extension. To evaluate the effect of growth form, we categorised native taxa into emergent and submersed/floating habits, based on where the majority of their foliage is typically found. To evaluate the effect of provenance, we split our data into native or exotic/hybrid species.

Importance values (IV) were calculated for each species in each sampling period and pond. Importance values were calculated on subsampled data by summing relative frequency and relative cover. An NMDS ordination of ponds in both time periods was performed using species with summed importance values of at least 0.05 across the dataset (out of a possible maximum of 2). NMDS was performed using the Sorensen distance matrix in PCORD using the ‘slow and thorough’ option, with random starting coordinates and 50 runs (McCune and Mefford 2006).

We calculated pond-scale species richness and Pielou’s evenness on subsampled data for all taxa in each time period (Beisel et al. 2003). We also calculated pond-scale richness values that excluded exotic and invader species. Results of analyses were not qualitatively different, so we only present total richness. We evaluated pairwise similarities amongst all ponds using subsampled data and calculated Bray-Curtis similarity on log-transformed frequency data. Differences in richness and evenness across time were evaluated by mixed-model ANOVAs, with age, year and their interaction as fixed variables and pond as a random variable. Similarity differences across time were evaluated via paired-t-tests; we tested changes amongst all 22 ponds and also tested changes within pond groups binned by age (‘young’ vs. ‘old’). These tests were performed after ensuring that data satisfied assumptions of normality.

We calculated proportional changes in richness and evenness for each pond to serve as response variables in the analyses of community change. We did not calculate a cover-change metric due to differences in sampling months and estimation methods between the 1982 and 2010/2011 surveys. As we were interested in the impact of each invader on community change over 28 years, we performed five mixed-model ANOVAs to evaluate how each invader contributed to richness and evenness change. We used the invaders’ cover values in 2010/2011 for these analyses. In each model, the fixed predictors were the target invader’s cover in 2010/2011, a combined metric summing the cover of the other four invaders, pond age and interactions between those three factors. Interactions were removed if they were not significant ($p > 0.05$). We also modelled the relationship between *Phragmites australis* and richness and evenness change in young ponds using simple linear regression.

We investigated whether combined invader cover in 2010/2011 was explained by other continuous pond characteristics (shoreline disturbance, average depth or area) using a stepwise regression model. The best model was selected via forward selection

and lowest AIC score. We compared pond area covered by each of our invaders in 2010/2011 across the two pond ages via a Wilcoxon test.

Prior to ANOVA and regression analyses, 2010/2011 biotic proportion cover variables and proportion shoreline disturbance were arcsine(sqrt)-transformed and depth and area were log-transformed to approximate normality.

Patch-scale surveys

A subset of species in this wetland complex, regardless of their status as invaders, form dense emergent, often clonal patches that may (but do not necessarily) exclude other species. To evaluate the effects of monodominant emergent taxa, we performed additional sampling in 2011 in patches dominated by each of four taxa: three invaders (*Typha × glauca*, a native-exotic hybrid, *Phragmites australis*, an exotic and *Cephalanthus occidentalis*, a native) and one additional native species (*Schoenoplectus acutus*). We chose *Schoenoplectus acutus* rather than our other native invader (*Persicaria hydropiperoides*) because *S. acutus* has a more similar habit to the invasive grass species (*Phragmites australis*). Each of the four selected taxa forms monodominant stands, which we define as dense, largely monospecific emergent patches of vegetation, in many shallow ponds in the Miller Woods wetlands. We selected six ponds that each contained at least two of our focal species (Suppl. material 1: Figure S1), so that each focal species was sampled within at least three ponds. Within patches of our focal species, we placed three or four 0.5×1 m quadrats along an 8–10 m transect for at least 37 quadrats across all ponds. Within each quadrat, we recorded percent cover and number of individuals of all species, water depth, light availability at three points using a LI-COR LI-250A light meter and the height of the tallest focal species individual. In every pond, we additionally sampled three transects (twelve quadrats) of reference areas – areas not dominated by any of our focal species – in comparable water depths as close as possible to our focal patches (Suppl. material 1: Table S5).

For 0.5-m² patch quadrat data, we calculated richness and Pielou's evenness of each quadrat using individuals. Quadrat-level richness and evenness were compared amongst patch types using nested, mixed-model ANOVAs. Pond and transects nested in ponds were included as random variables and patch type (monodominant species) was a fixed variable – we did not have enough replication to consider the patch-by-pond interaction. Variables were log-transformed before analysis to satisfy assumptions of normality. When the overall model was significant ($p < 0.05$), we used Tukey's HSD test to evaluate significant differences between patch types.

To evaluate the effect of monodominant species on richness accumulation, we calculated sample-based rarefaction curves for all quadrats sampled in each patch type (*Typha × glauca*, *Phragmites australis*, *Cephalanthus occidentalis*, *Schoenoplectus acutus* and reference patches) to evaluate study-wide richness. Analytically estimated richness and standard errors from randomisation trials were selected at 37 quadrats - the number of quadrats sampled for *Cephalanthus occidentalis*. We also calculated richness

Table 1. Results of mixed-model ANOVAs explaining pond-scale total species richness and species evenness between two time periods (1982, 2010/2011) and two categorical age groups of ponds (young, old). Pond was included as a random effect.

Response	Source	DF	F Ratio	P
Total richness	Age	1	0.720	0.4062
	Year	1	5.559	0.0287*
	Age * Year	1	13.240	0.0016*
Species evenness	Age	1	0.085	0.7734
	Year	1	1.674	0.2104
	Age * Year	1	3.122	0.0925†

* $p < 0.05$; † $p < 0.10$.

at an intermediate scale by analytically estimating richness at 12 quadrats for each patch type/pond combination where at least 12 quadrats were sampled. We compared 12-quadrat level richness estimates in a mixed model ANOVA that included patch type as a fixed effect and pond as a random effect.

Results

Three exotic and seven native taxa significantly increased in frequency of occurrence over the 28 years of this study (Suppl. material 1: Table S1). The exotic taxa *Lythrum salicaria*, *Phragmites australis* and *Typha × glauca*, each emergent aquatic species, were each found in at least 15 of the 22 ponds surveyed in the 2010 period. Both *Phragmites* and *Typha* were present in the 1982 sample, while *Lythrum* has colonised the wetland complex in the ensuing 30 years. Native ‘increaser’ species varied in habit from emergent aquatic (*Cephalanthus occidentalis*, *Persicaria hydropiperoides*, *Zizania palustris*), floating aquatic (*Nymphaea odorata*), submerged aquatic (narrow-leaved *Potamogeton* spp., *Utricularia macrorrhiza*) and shoreline taxa (*Carex* spp.). Fifteen native taxa, including the monodominant species *Schoenoplectus acutus*, decreased significantly in frequency of occurrence. Thirteen taxa did not change significantly in frequency of occurrence across ponds. ‘Decreaser’ and ‘no change’ taxa each also included emergent, floating/submerged and shoreline taxa.

Pond-scale richness was significantly predicted by year ($p = 0.0287$) and the interaction between pond age and year ($p = 0.0016$, Table 1). Richness increased over time in young ponds and decreased in old ponds (Figure 1A). Richness was greater in old ponds than in young ponds in the 1982 sampling period, but that difference disappeared by the recent survey period. Pond-scale evenness did not change significantly over time, although the interaction term of the two-way mixed model ANOVA was marginally significant (Table 1, Figure 1B). Bray-Curtis similarity increased over time across all ponds but decreased in young ponds, resulting in significantly greater Bray-Curtis similarity amongst old ponds than amongst young ponds in the resurvey ($t = -1.96$, $p < 0.05$).

The final NMDS ordination of 22 sites in each time period, based on species importance values, had a stress of 12.984 after 399 iterations (Figure 2). Axes 1, 2 and 3

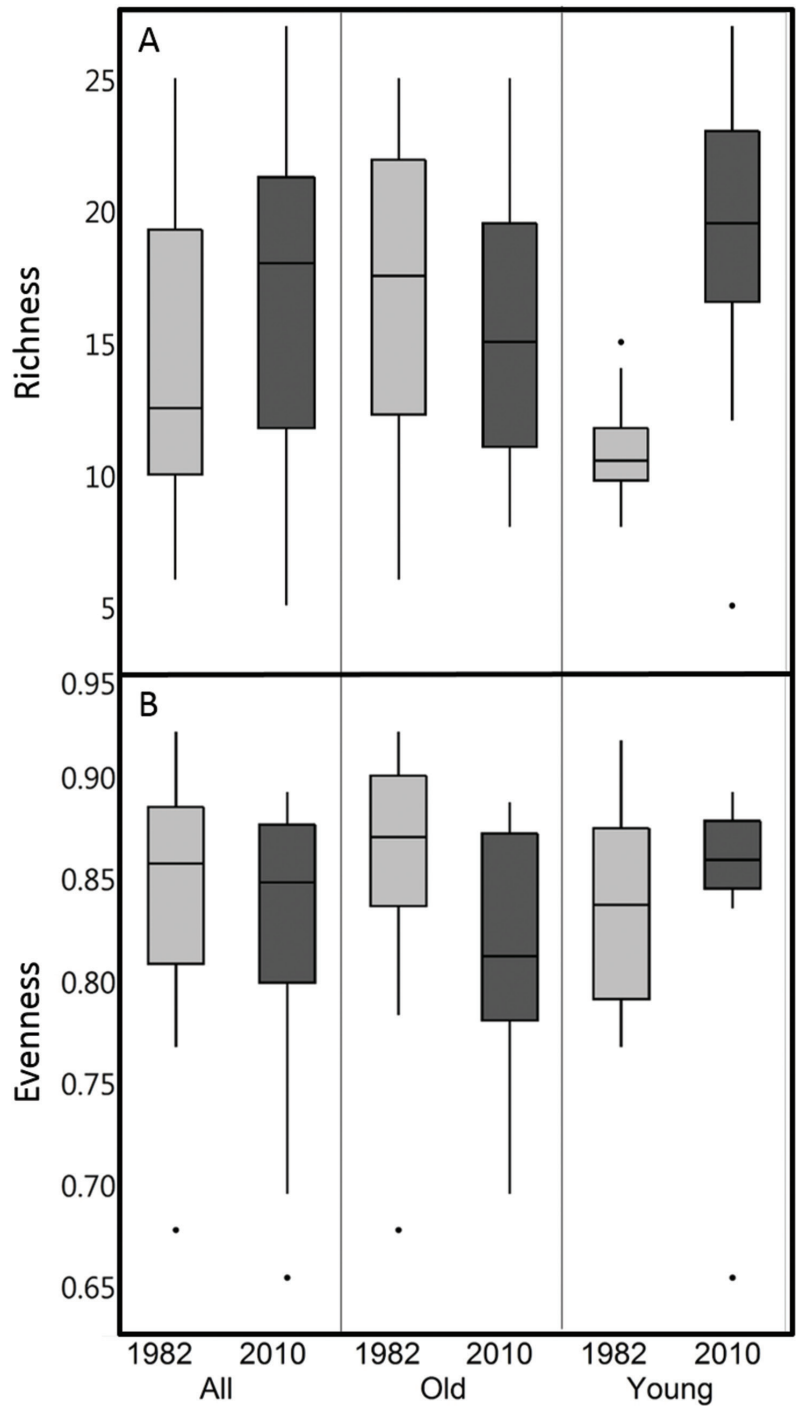


Figure 1. Richness and evenness of pond macrophytes in 1982 (light grey) and 2010/2011 (dark grey). Medians, first and third quartiles, interquartile ranges and outliers are shown. Richness and evenness differences were evaluated via ANOVAs (see Table 1).

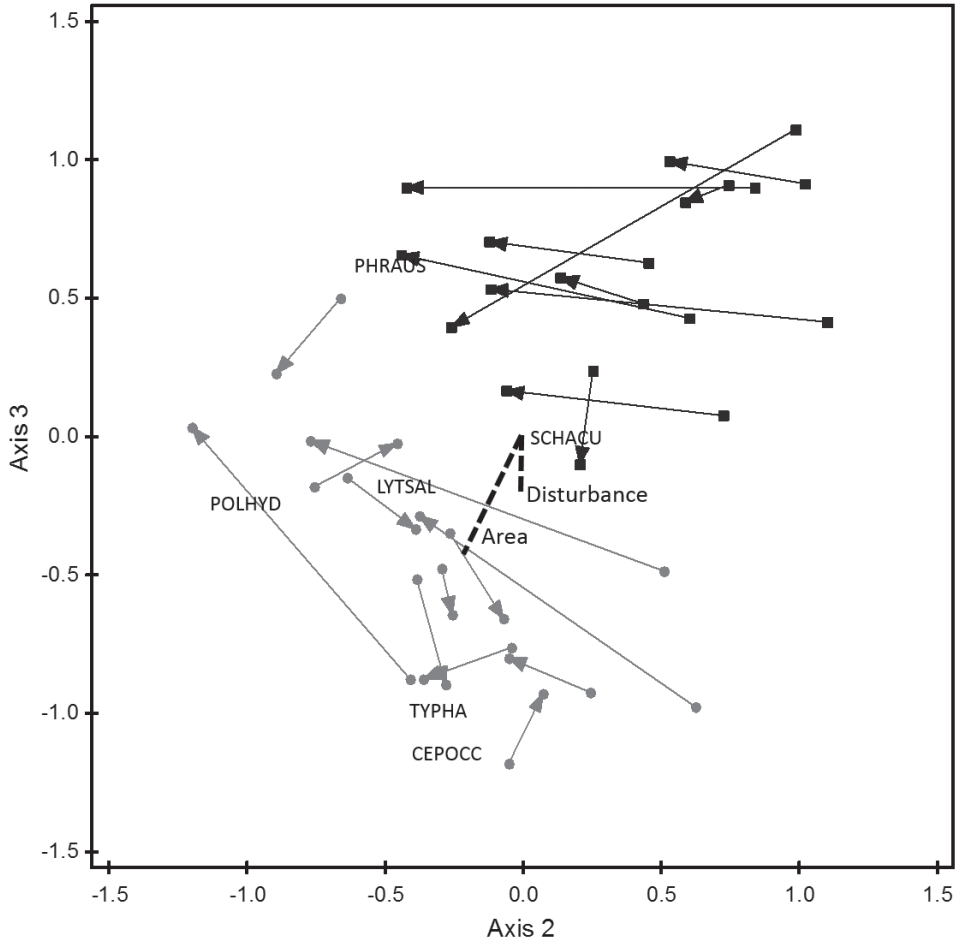


Figure 2. NMDS ordination of 22 sites in two time periods (1982 and 2010/2011) based on species' importance values. Grey symbols and arrows represent "old" ponds, black symbols and arrows indicate "young" ponds. Arrows pair the same site in two time periods, the arrowhead indicates the later (2010/2011) sample. Dashed lines indicate biplots of variables with $r > 0.300$. Species centroids of invader and monodominant taxa are indicated. PHRAUS: *Phragmites australis*, SCHACU: *Schoenoplectus acutus*, LYTSAL: *Lythrum salicaria*, POLHYD: *Persicaria hydropiperoides*, CEPOCC: *Cephalanthus occidentalis*, TYPHA: *Typha × glauca*.

explained 0.194, 0.294 and 0.362 of the variance in the dataset; we present those that explained the most variance, i.e. Axes 2 and 3. "Young" and "old" pond sections separated in ordination space. Both pond area and shoreline disturbance were correlated with decreasing values on either or both axes, as indicated by the ordination biplot. Species centroids of invader and mono-dominant taxa indicate that older ponds are relatively dominated by *Cephalanthus occidentalis* and *Typha × glauca* whereas young ponds have more *Phragmites australis*. Within most (9 of 10) young ponds, there was a convergence towards increased dominance by *P. australis* between the two time periods.

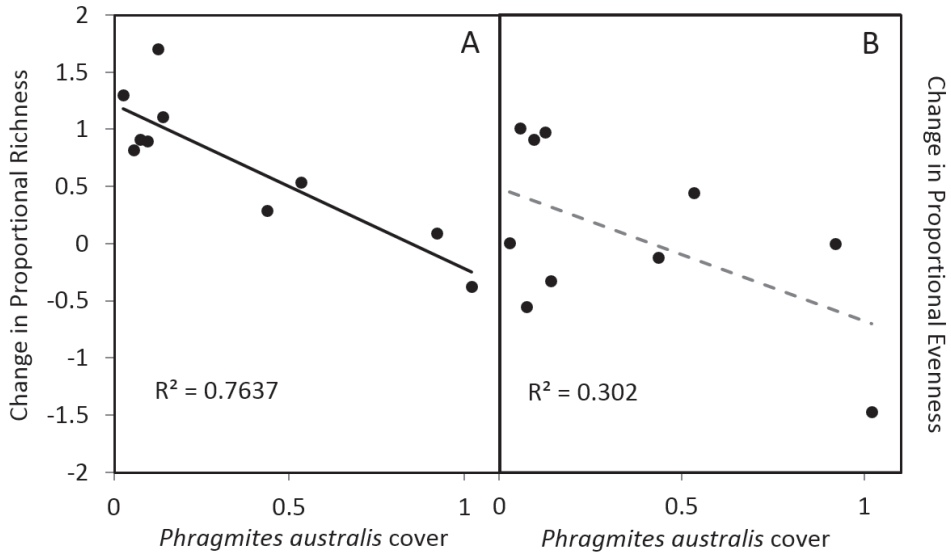


Figure 3. Relationship between *Phragmites australis* cover (as proportion of area sampled) and the proportional change in richness (**A**) and evenness (**B**) in young ponds. The solid line indicates a significant ($p < 0.05$) relationship and dashed line indicates $p < 0.10$.

Invaders reached their greatest cover in ponds that were altered by railroads or roads (Suppl. material 1: Figure S2). The best stepwise model explaining invader cover in 2010/2011 was pond age, fraction of shoreline altered and their interaction, with a final adjusted R-squared of 0.6789. Disturbance was positively related to invader cover and that relationship was steeper in young ponds than in old ponds. Invaders differed in the extent to which they dominated ponds; *Lythrum salicaria* and *Persicaria hydropiperoides* covered less than 1% of pond area, native *Cephalanthus* covered ~2.5% and *Typha* (hybrid) and *Phragmites* (exotic) covered around 10% each (Suppl. material 1: Table S2). *Phragmites* was significantly more abundant in young ponds, whereas *Cephalanthus* and *Typha* were significantly more abundant in old ponds.

Of the five species identified as ‘invaders’ in this system, only *Phragmites australis* cover was related to changes in richness (Suppl. material 1: Table S3). The effect of *Phragmites* cover was significantly different across age sections, where increasing cover in young ponds, but not old ponds, depressed richness gains. No ponds with greater than 25% *Phragmites* cover gained species, regardless of pond age. Only the interaction between *Typha* cover and section was significant in predicting change in evenness (Suppl. material 1: Table S3). When young ponds were modelled separately, increasing *Phragmites* cover was significantly negatively related to richness gains ($p = 0.009$, Figure 3A), such that ponds with greatest *Phragmites* cover increased in richness the least between survey periods. Increasing *Phragmites* cover was also negatively related to evenness change, although this relationship was only significant at a $p = 0.01$ level ($p = 0.09$, Figure 3B). The relationships for change in richness and change in evenness in young ponds, associated with increasing cover of *Phragmites*, are not consistent with

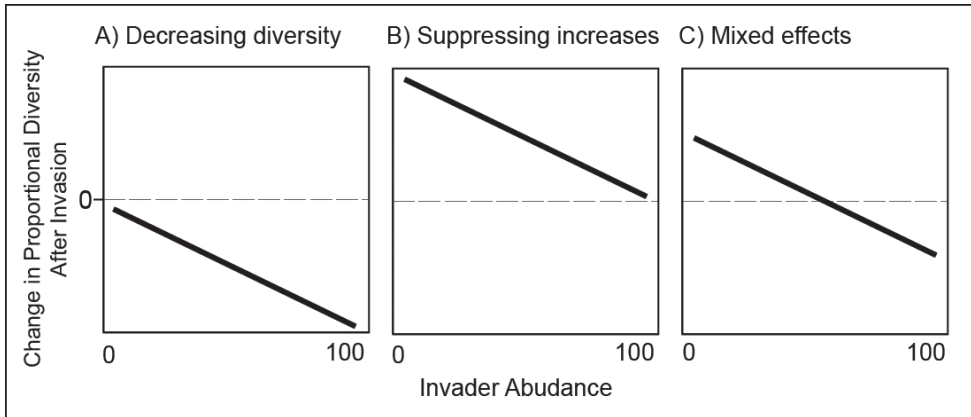


Figure 4. Conceptual figure illustrating three possible ways invasive species abundance could negatively correlate with changes in diversity. **A** At high abundance, invaders could cause declines in diversity over time. **B** At low invader abundance, diversity increases through natural processes, but at high abundance, invaders prevent arrival of new species. **C** A combined model, where richness increases in the absence of invaders and invader presence above a threshold causes declines in diversity over time. Note that these hypothesised relationships may not be linear but may include threshold processes.

“decreases” in diversity (Fig. 4A), but instead more consistent, respectively, with “dampening increases” and “mixed effects” (Figs 4B, C).

Native species in this system were more likely to decrease or have no change than increase in frequency (7 of 35 species were increasers, while all three exotics were increasers, Suppl. material 1: Table S1). This difference amongst natives was significant when evaluated by a Fisher Exact Probability Test with the Freeman-Halton extension ($P_A = 0.014$; $P_B = 0.014$). A Fisher test revealed no association between growth form (emergent or submersed/floating) and status of change over 28 years ($P_A = 0.907$; $P_B = 0.907$).

The four monodominant taxa (*Cephalanthus occidentalis*, *Schoenoplectus acutus*, *Phragmites australis*, *Typha × glauca*) altered their abiotic environments similarly. Each covered about 70% of the quadrat area, blocking 73–88% of the light reaching the water surface (Suppl. material 1: Table S4). Within quadrats, richness ranged from 2.3 to 3.3 species per 0.5-m² quadrat across patch types (Figure 5A); native *S. acutus* and reference patches supported the largest richness while *T. × glauca* (native-exotic hybrid) the lowest. These differences were not significant when evaluated using a mixed-model ANOVA. Richness aggregated across 12 quadrats was also greatest in *S. acutus* and reference quadrats (Figure 5B). Differences in 12-quadrat aggregated richness were significant as evaluated by a mixed-model ANOVA ($F = 3.81$, $p = 0.035$, model $R^2 = 0.58$), although pairwise differences were not significant. Total richness across 37 quadrats, as estimated by Mao-tau, was greatest in reference quadrats, followed in decreasing order by *S. acutus* (native), *P. australis* (exotic), *T. × glauca* (native-exotic hybrid) and *C. occidentalis* (native) quadrats (Figure 5C). Quadrat-level evenness amongst 0.5-m² quadrats was greatest in *C. occidentalis* and reference quadrats (0.78 and 0.67, respectively) and lowest in *S. acutus* quadrats (0.4, Suppl. material 1: Figure S3).

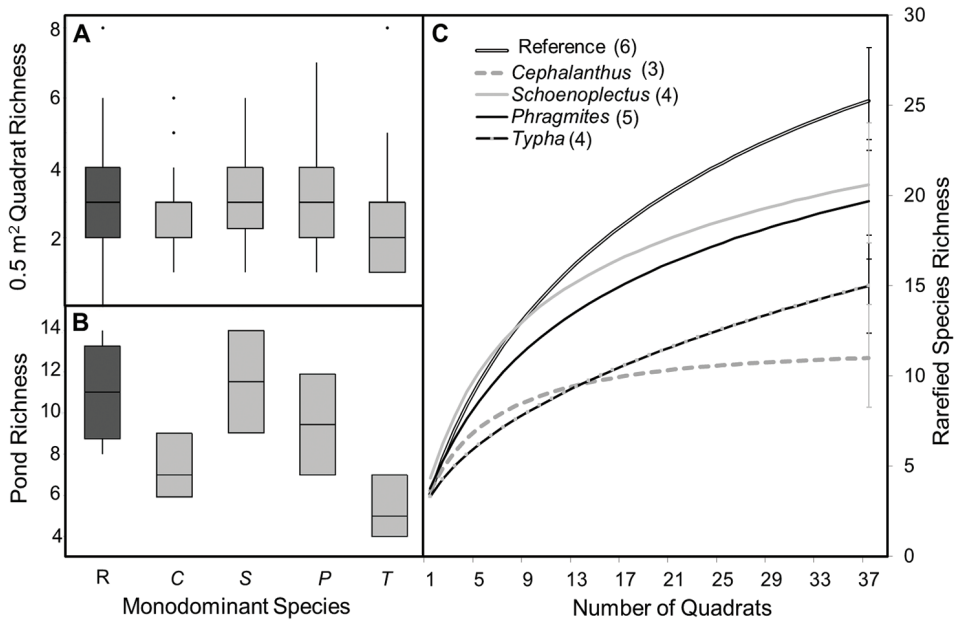


Figure 5. Richness at three scales in patches dominated by *Cephalanthus occidentalis* (C), *Schoenoplectus acutus* (S), *Typha × glauca* (T), *Phragmites australis* (P) or reference areas (R). **A** 0.5 m² quadrats **B** aggregated pond-level richness (12 quadrats) **C** Mao-Tau sampling-richness relationships, with the number of ponds each type was sampled in indicated in parentheses. Error bars indicate standard deviation at 37 quadrats. Patch type (monodominant species) was a significant predictor of pond-level richness as evaluated via a mixed-model ANOVA ($F = 3.81$, $p = 0.035$, model $R^2 = 0.58$).

Discussion

This study provides insight into two major unresolved questions in invasion biology. Can species impacts be predicted based on their provenance? Do species invasions, regardless of provenance, decrease biodiversity at local scales? In this wetland complex, monodominant emergent invaders have likely altered the trajectory of pond community change over 28 years but in ways that are not fully consistent with an expectation of biodiversity loss or of categorical variation by provenance. Invader cover is only minimally correlated with changes in evenness over time and, rather than decreasing richness, invader cover (*Phragmites australis*) is correlated with suppression of richness gains in some ponds. Further, in this study, invaders that entered the community recently (“exotic invaders”) or were present at low levels historically but increased following human disturbance (“native invaders”), do not show strong categorical differences in how they impact these communities with respect to changes in diversity at local, quadrat scales. However, exotic and native invaders altered temporal trajectories of richness in ponds over 28 years.

Cover of *Phragmites australis* in ponds during the resurveys was negatively correlated with proportional change in species richness in young ponds, but this was not because

of a loss of species over time. Indeed, in our study, average net richness of species in ponds increased between surveys. To understand this apparent contradiction, it is useful to consider three qualitative ways that a negative correlation between invader cover and change in biodiversity could manifest in communities that have shown a net increase in richness between surveys (Fig. 4). A single biodiversity measure, such as richness, could show a loss of species associated with high cover (Fig. 4A), but alternatively, change in richness could be 'dampened,' such that the most invaded ponds do not increase in richness, whereas the least invaded ponds do (Fig. 4B); finally, a mixed effect could occur, such that the least invaded ponds increase in diversity, whereas the most invaded decrease (Fig. 4C). Our results, with respect to species richness, are largely consistent with diversity increases being dampened and not with loss or mixed effects, whereas change in species evenness is most consistent with mixed effects. One possible explanation for these patterns is that invasion of *Phragmites* has altered the successional trajectory of these young ponds; a proposition supported by the consistent movement of ponds towards *Phragmites* in an ordination of compositional change in young ponds (Fig. 2).

Regardless of the mechanism, however, these patterns raise an important challenge for ecological studies of long-term change – namely, determining the relative influence of invaders versus other changes in the environment in driving change in diversity. In the meta-analysis by Vellend et al. (2013), the effect of invasion (seven studies) was a decrease in diversity, whereas the effect of recent disturbance (and presumably the early stages of succession – thirteen studies) was an increase in local diversity. More studies, particularly those that explicitly consider both types of change simultaneously will be needed to understand this issue better. We believe that the qualitative alternatives for change in diversity presented here (Fig. 4) can provide a point of context for framing these studies. Better understanding this issue will likely become increasingly important in the context of ongoing changes in climate that are matched with new species invasions.

This lack of evidence for significant loss of diversity, in spite of pronounced invasions, not just in young ponds but across our broad set of ponds, might be due to several factors – in addition to the possibility of pond succession, described above. Many uncommon taxa are still present in this wetland complex and no 'common' taxa were extirpated from the ponds we surveyed during the 28-year period. It is possible that seasonal and between-year variations in water levels may provide opportunities for continued survival or regeneration of species with differing requirements, maintaining some degree of balance between invading emergent stands and diverse sedge meadows, as elsewhere in the Great Lakes (Wilcox et al. 2008). It is also possible that these ecosystems are simply heterogeneous enough (within a given season or year) to support many taxa, in spite of the dominance of a few highly abundant species. Another possibility is that the deeper waters of some ponds might provide a refuge for enough species and that the impacts of these emergent shallow-water invaders are muted. Regardless of the mechanism, these alternative outcomes in changes of biodiversity measures should be relevant to consider whenever a system's metric of interest (such as species richness) changes over time.

Native and exotic invaders do not show consistent differences in how they impact these ecosystems across all biodiversity measures or spatial scales. At the scale of entire

ponds, the exotic invader *Phragmites australis* had the greatest impact on change in richness over time. However, *Phragmites australis* has a pond-scale impact not because of unique within-patch processes, but because of the number and size of patches it had invaded. At the scale of individual habitat patches, there was no evidence that native and exotic monodominant species had categorically different effects on plant diversity. Although neither natives nor exotics showed categorical differences at this scale, species accumulation measures showed that both natives and exotic invaders were associated with reduced diversity relative to uninvaded reference areas. In other studies, both *T. × glauca* and *P. australis* are reported to decrease plant richness in freshwater wetlands (Meyerson et al. 2000; Angeloni et al. 2006; Mitchell et al. 2011) and so might native monodominant species. Given the similar reductions in light we found, in combination with other work finding similar environmental changes between dense native and exotic emergents that form dense patches (Bunch et al. 2010), we can conclude that the habit of these species – forming dense patches that block light and crowd out other species at both the water and soil surface – is more important than whether those species are native or exotic. Other wetland studies have reached similar conclusions; species provenance is not a consistent indicator of whether or not an individual species will be common and dominant. Instead, individual species traits are apparently better predictors of species dominance in these habitats (Houlahan and Findlay 2004; McGlynn 2009).

Historical disturbance in this wetland complex may have provided opportunities for invaders to colonise and spread, ultimately leading to different species accumulation trajectories in the recent past. As a consequence, it is difficult to disentangle the extent to which patterns observed are driven by the invaders or instead driven by disturbance, per se, which may have also benefited the invaders, i.e. it is difficult to know if the invaders are ‘drivers’ or ‘passengers’ of observed change. We do know that invader abundance in these ponds is positively correlated with shoreline alterations and hydrological disturbances; this is particularly true in younger ponds, where the large differences in invader cover are apparent between ponds with and without disturbed shorelines. Differences in the responses observed in younger and older ponds are consistent with the important differences these ponds have with respect to their natural history but might also reflect differences in susceptibility to the influences of invasion with successional stage. In both pond types, however, the initial creation of roads and railroads may have altered the environment in a manner known to be favourable for emergent wetland vegetation, including the three exotic invaders studied here (Galatowitsch et al. 1999). Railroad and road rights-of-way can also increase the movement of weedy propagules via human and other animal dispersers. It is possible that disturbances could also have directly affected the dynamics of non-invader species in this wetland complex. Alterations of hydrology leading to aquatic dispersal limitation or loss of populations and habitat during the initial disturbance could have affected trajectories of species change in these ponds (Trombulak and Frissell 2000; Houlahan et al. 2006).

Given the highly dynamic nature of wetland habitats, it is possible that invader-induced suppressions of increases in richness could have long-term negative impacts

on biodiversity in these wetlands, particularly since there can be time lags before some impacts are manifest (Jackson and Sax 2010). To preserve diversity in this wetland complex and others like it, managers may need to evaluate the necessity of mapping and controlling the spread of both native and exotic emergent invaders, regardless of provenance. This includes early detection efforts, which are critical when a known invader is approaching an uninvaded area. Whenever possible, managers should integrate knowledge of historical (pre-settlement) abundances in evaluating which species should be monitored rather than focusing exclusively on exotic invaders. Indeed, in some cases, the most impactful invaders may be native species (Carey et al. 2012).

Although our results cannot resolve the debates regarding the importance of species provenance or the impact of exotic species on local diversity, they do provide an important point of reference for these debates and highlight the potential interactions between them. The recent meta-analysis by Vellend et al. (2013) found that sites that had been invaded showed a net decrease in richness over time, but this result was based on only seven studies. Our results provide an important counter-example, indicating that sites colonised by exotic species need not experience reductions in local richness (as measured here at the pond scale). Here, instead, invader cover of *Phragmites australis* was correlated with suppression of richness gains. This suggests that change in local richness following invasions might ultimately be idiosyncratic - a conclusion supported by the more general results across all local sites studied by both Vellend et al. (2013) and Dornelas et al. (2014b). Likewise, although species' provenance might be important in predicting impacts (Simberloff et al. 2011; Fridley and Sax 2014), it did not have consistent categorical predictive power in these communities. In this context, it is perhaps less surprising that exotic species in our study were not associated with decreases in species richness of ponds. Decreases in richness, following arrival of exotic species, might only be expected in cases when categorical differences between natives and exotics are large and apparent, but this can only be assessed when more studies directly comparing the impacts of native and exotic 'invaders' have been conducted. Future observational and experimental research is needed to continue to resolve these two debates.

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Supplementary material I

Supplementary tables and figures

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Data type: species data

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Undelivered risk: A counter-factual analysis of the biosecurity risk avoided by inspecting international mail articles

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Abstract

International mail articles present an important potential vector for biosecurity and other regulatory risk. Border intervention is a key element in Australia's biosecurity strategy. Arriving international mail articles are inspected and those that are intercepted with biosecurity risk material are documented, including the address to which the article was to be delivered. Knowledge about patterns in the intended destinations of mail article permits more detailed biosecurity intervention. We used geo-location software to identify the delivery address of mail articles intercepted with biosecurity risk material from 2008–2011. We matched these addresses with demographic data that were recorded at a regional level from the Australian Bureau of Statistics 2011 Census and used random forest statistical analyses to correlate various demographic fields at the regional level with the counts of seized mail articles. The analysis of the seizure counts against demographic characteristics suggests a high correlation between having higher numbers of university students that speak a particular language in a region and higher quantities of intercepted mail articles destined for that region. We also explore metropolitan and regional patterns in the destinations of seized materials. These results can be used to provide information on policy and operational actions to try to reduce the rate at which mail articles that contain biosecurity risk material are sent to Australia.

Keywords

biosecurity, random forest, international mail, demographic analysis, population characteristics, Australian Bureau of Statistics 2011 Census of Population and Housing, spatial, prohibited goods, intercepted mail, risk profiling, compliance behaviour, data mining

Introduction

Biosecurity is the management of risks to the economy, the environment and the community, of pests and diseases entering, emerging, establishing or spreading (see, e.g. Craik W and Palmer D and Sheldrake R 2017). Australia's unique flora and fauna and strong reliance on agriculture make it specifically sensitive to invasive pressures, hence, many food, plant and animal products are considered to present a substantial biosecurity risk as they may be vectors for invasive pests. Its world-class biosecurity system is multilayered and complex, comprising activities undertaken offshore, at the border and onshore, by a broad range of participants that includes all Australian governments, industry, exporters and importers, farmers and other stakeholders (Craik W and Palmer D and Sheldrake R 2017). Australia's Department of Agriculture and Water Resources (hereafter, the department) plays an integral role in the biosecurity system. The department is the regulatory authority and inspectorate that is responsible for maintaining border biosecurity, amongst other things, focusing on biosecurity to protect agriculture, social amenity and the environment. It carries out this important responsibility via a suite of activities, including screening, monitoring, inspection and, when necessary, litigation. For example, the department sets out the conditions under which food, plant and animal products may be imported in the online Biosecurity Import CONditions database, BICON (Department of Agriculture 2018).

Incoming mail presents an important threat to biosecurity because it provides a pathway by which pests can enter (Meyerson and Reaser 2002). In 2014, approximately 176 million mail articles entered Australia, via one of four international gateway facilities, located in Sydney, Melbourne, Brisbane and Perth. The department performs both targeted and random inspections of incoming mail at each of these facilities, amongst other activities. Generally speaking, the intervention is carried out in order to intercept regulated pests, to verify the compliance of pathways with Australia's biosecurity legislation, to monitor the international environment and to detect and deter malfeasance. Screening and inspection at the gateway facilities may be by x-ray, specially trained detector dogs or opening the article and examining the contents. Mail items that are found to contain biosecurity risk material are seized and treated according to biosecurity policy (Department of Agriculture 2016a). The details of the seized item, including the location to which it was addressed, are recorded.

Here we report a counterfactual analysis of the factors common to the delivery addresses of seized mail articles, by exploring the relationship between population characteristics in these locations and interception data. The analysis is counterfactual in the sense that we are examining the patterns of biosecurity risk that was *not* delivered; the mail articles were seized upon arrival. The motivation for the analysis reported

in this paper was to better understand the patterns of destinations of seized materials and the characteristics of the regions of higher seizure risk. Prior to this analysis, there was some anecdotal evidence linking the importation of particular commodities, via the post particularly, with areas of large numbers of young people attending university. This project allowed a more rigorous assessment of this evidence, by investigation of the assumptions to see whether or not they are reflected in the historical data and to identify any other associations between population groups and the importation of high risk biosecurity goods, that are not yet known.

This knowledge would enable the department to target public relations campaigns that would focus upon informing the public about the risks and laws around the importation of foreign materials into Australia.

Methods

Data preparation

We used two sets of data to explore the relationship between the delivery addresses of seized articles and population characteristics or demographics of the local area.

First, the department's Mail and Passenger System (MAPS) database provided data about mail articles seized from 1 January 2008 until 31 December 2011, including a variety of characteristics of the article, the most relevant of which were the intended delivery address, which could be used for geocoding and the nature of the seized goods. The second set of data, provided by the Australian Bureau of Statistics (ABS), contained a range of demographic fields of consideration from the 2011 Australian Census. These were provided at the level of statistical unit 2 or SA2 polygons, one of the main structures within the Australian Statistical Geography Standard framework, a framework designed to enable consistent and comparable publication of statistics. SA2s are medium-sized geographical units intended to represent a community that interacts together socially and economically (Australian Bureau of Statistics 2016a). They are the smallest area for the release of many ABS statistics. There are 2,214 SA2 spatial units within Australia with populations ranging from 3,000 to 25,000. Visual comparisons as well as exploratory analysis at the finer grade of Statistical Area 1 (SA1) suggested that the SA2 was a more appropriate unit of analysis due to the increased number of seizures per unit, while not diluting the key patterns and relationships.

There is a large number of Census fields available for the analysis of individuals in the Australian population, therefore the analysis needed to focus on a smaller number of Census fields for the project to be feasible. *Profiles* were therefore developed of persons or groups associated with the admission of high risk biosecurity goods into Australia. Risk factors for the profiles were based on known intelligence and anecdotal evidence, provided by internal departmental studies, internal Customs studies and broader anecdotal evidence of links between imports and specific demographic groups

(Department of Agriculture 2016b, Maller C, Kancans R and Carr A 2007, Kancans R, Stenekes and Benedictos T 2010). In particular, this anecdotal evidence included a number of assumptions linking demographics and importation of particular commodities, in particular, that higher seizure incidences often occur in areas with large numbers of young people attending university.

Anecdotal and empirical research indicated that:

- culturally significant events may be the catalyst to the importation of high risk goods (plant and animal) through the postal system (e.g. cultural and religious festivals or events);
- culturally significant plants may be the catalyst to the importation of high risk plant material through the postal system;
- communication is a barrier to informing and educating persons of culturally and linguistically diverse (CALD) backgrounds about high risk biosecurity behaviour relating to the importation of plant and animal material through the postal system;
- cohorts of CALD persons may distribute biosecurity risk material due to close relational ties and spatial proximity;
- CALD persons studying in Australia are considered a high risk group; and
- CALD persons engaged in agricultural production could be a high biosecurity risk group due to the proximity to commercial agriculture.

The considerations discussed above led to a choice of ABS Census fields regarded as potential risk factors of individuals for the importation of biosecurity risk items which included:

- language spoken at home
- student attending an educational institution (university or other tertiary institutions)
- full-time or part-time attendance status of educational institution
- age in 5 year groupings
- people employed in industries related to horticultural production, including nursery and floriculture, mushroom and vegetable growing and fruit and nut tree growing.

In addition to these fields, the list of census fields was broadened to include those that had not been identified in the anecdotal evidence, but may still be important. These other fields are related to socio-economic circumstances including household characteristics, income levels and employment; those commonly used to describe a population. Land use within the SA2 was also a desirable field, due to the differing impact of biosecurity risk material for certain land uses, for example, primary production or parkland. This information was available by mesh block, the smallest geographic unit available from the ABS (Australian Bureau of Statistics 2016a). These units were aggregated to provide proportions of each land use type for each SA2.

The full set of census fields considered are included in Table 1. For the purpose of analysis, counts of each level of the census field were considered separately as

dummy variables, so there were technically 2854 variables used in the model to represent these 32 fields.

In order to be able to relate the seizure counts and these fields, we counted the number of seized articles that were addressed to locations within each SA2 polygon. This count required a match between the delivery addresses and the SA2 locations, which was performed using the G-NAF (Geographic National Address File) provided by Navigate¹. This operation took consignee details addresses from items seized at the border and assigned geospatial parameters to it, namely the latitude and longitude and the ABS SA2 and SA1 areas. Overall, the geocoder worked as expected. Although failure rates were initially high, this was, however, more likely due to poor address data (e.g. special or foreign characters not readable by the G-NAF). This poor data quality was fixed through a thorough cleanse of the data. Once the geocoding was completed, this provided a key point of data that was unique across the MAPS data and the census information, namely the SA1 and SA2 locations. Using this standard data field, we were able to join and analyse the data with more accuracy.

Of the 404,873 seizure records in the period of consideration, 307,627 (76%) could be matched to a unique SA2 area. Failures to match were for a range of reasons, including that the international sender address was incorrectly included as the recipient address, that the address was poorly spelled or that the address was fake. Of the 307,627 matched records, 161,390 (52%) contained risk articles that either lacked appropriate Customs declaration or were misdeclared. These records were used for analysis – correctly declared items that were seized were not included.

These seizure counts per SA2 polygon were then matched with the equivalent demographic fields in order to explore the demographic characteristics of high seizure areas.

Random forest analysis

In seeking to determine which demographic fields are related to high seizure areas, one challenge is the very large number of possible demographic relationships. Therefore, a robust methodology was required to determine which were most closely related to increased seizures. A flexible model was also needed, as these relationships are not necessarily linear nor consistent across demographic fields. Tree-based models are valuable in exploratory cases such as these, because they allow for complex relationships between predictors and outcomes, including interactions between predictors in the way they affect the outcome (Hastie et al. 2009). We can create a tree that progressively splits each group of observations into two subgroups, based on the level of individual demographics fields. The choice of splits can be optimised automatically in software to best separate those with high and low risk of seizures. Note that the seizure outcomes used in these models was the rate per 100,000 of population, to allow for differences in the population in each SA2. The choices of splits yield useful information about the importance of the demographic fields in determining those areas with high levels of seizures. Complex interaction patterns are also naturally incorporated into tree models.

Table 1. Census fields considered in the analysis.

Category	Code	Census field
Language	LANP	Language Spoken at Home
	ENGLP	Proficiency in Spoken English/Language
	ENGP	Proficiency in Spoken English
Diversity	CITP	Australian Citizenship
	YARP	Year of Arrival in Australia
	BPLP	Country of Birth of Person
	ANC1P	Ancestry 1 st Response
Education	TYSTAP	Educational Institution: Attendee Status
	TYPP	Type of Educational Institution Attending
	HEAP	Level of Highest Educational Attainment
Household	HCFMD	Family Household Composition (Dwelling)
	CDCF	Count of Dependent Children in Family
	STRD	Dwelling Structure
	NEDD	Type of Internet Connection
	MDCP	Social Marital Status
	VEHRD	Number of Motor Vehicles (ranges)
	NPRD	Number of Persons Usually Resident in Dwelling
	TEND	Tenure Type
	MV1D	Household One Year Mobility Indicator
	RNTRD	Rent (weekly) Ranges
	MRERD	Mortgage Repayments (monthly) Ranges
Income	HIED	Equivalised Total Household Income (weekly)
	HIND	Total Household Income (weekly)
	INCP	Total Personal Income (weekly)
Employment	INDP	Industry of Employment
	GNGP	Public/Private Employer Indicator
	OCCP	Occupation
	POWP	Place of Work
	LFSP	Labour Force Status
Age	AGEP	Age in single years
Gender	SEXP	Sex
Landuse	N/A	Land use based on Mesh Block Category

It is possible to construct one such tree model for these data but over fitting is a genuine risk. As there is a relatively large number of potential demographic predictors available when fitting the model, it is possible to estimate the risk for the existing data very well, but the model may not be generalisable to other pathways. For example, it may highlight spurious relationships due to only a few unusual observations in this particular data set. One way to mitigate this problem is to create many trees based on random samples of the data and average the results of these, so the results are not sensitive to the specific data available. These kinds of models are called random forests, as they involve many trees generated from random samples of the data. These kinds of models have been shown to have very high performance (Fernández-Delgado et al. 2014) and the number of SA2s makes this approach feasible in this case. The

longitude and latitude of the centroid of each SA2 polygon was also included to allow for and assess spatial correlations (Mascaro et al. 2014). The particular random forests used for this analysis involved 5000 trees, with the minimum size at each terminal node set to 5.

All analysis used the open-source statistical environment R (R Core Team 2013), along with contributed packages randomForest (Liaw and Wiener 2002), sp (Pebesma and Bivand 2005), ggmap (Kahle and Wickham 2013), rgdal (Bivand et al. 2014), gstat (Pebesma 2004) and ggplot2 (Wickham 2009).

Results

Description of seizures

Total seizure numbers for the period are reported for each of 12 broad commodity categories and counts of these seizures are given in Tables 2 and 3, separated by state and region. Region in this case is defined using the ABS remoteness structures, which are based on a measure of relative access to services (Australian Bureau of Statistics 2016b). In order to identify patterns of dependence between the address locations and category (that is, whether certain states/regions are associated with more or less of certain seizure types) the cell deviations that contribute to a χ^2 -test were considered (Greenwood and Nikulin 1996). A cell deviation less than -2 or greater than 2 was considered evidence for a lack of independence; here we observe some deviations of 10 times this amount which would be highly unexpected if the categories and locations were truly independent. Based on the magnitude of these cell deviations, given in brackets, there were proportionally fewer Animal Products destined for Victoria (-28.9) compared with New South Wales (NSW) (10.1) and Queensland (29.3) and greater amounts of Plant/Plant Products (15.0), also compared with these states (-10.0, -12.8). Overall, there were greater amounts of Human Therapeutics destined for Victoria (21.9), Vegetable/Vegetable Products destined for NSW (8.5) and Contaminated Goods/Footwear/Packaging destined for Western Australia (16.1). There are increased numbers of Plant/Plant Product seizures destined for regional areas (19.4) compared with metropolitan areas (-8.6) and increased numbers of Fruit/Fruit Product, Vegetable/Vegetable Products and Mushroom/Fungi seizures destined for metropolitan areas (4.4, 4.6, 5.2) compared to regional areas (-9.4, -10.4, -10.8).

Random forest results

As the random forest approach involves the averaging of many tree models, no single tree or diagram can be used to display the relationship between the demographic data and seizure rates. However, it is possible to consider the effect of each key demographic

Table 2. Counts of seizures from 2008–2011 by broad commodity category and region.

Broad commodity category	Remote	Regional	Metropolitan
Animal Products	484	6553	40148
Biologicals	17	236	958
Contaminated Goods/Footwear/Packaging	84	1356	5655
Fruit & Fruit Products	63	1165	8741
Grains, Legumes & Nuts	100	1472	10537
Herbs & Spices	91	1284	7623
Human Therapeutics	136	2048	12451
Live Animals	1	27	119
Mushroom /Fungi	13	442	4333
Plant/Plant Products	700	11884	52200
Soil/Mineral Samples & Fertiliser	10	253	867
Vegetable/Vegetable Products	46	549	4950
Total	1747	27336	149183
Overall rate per 100,000 population	19.6	32.4	88.7

Table 3. Counts of seizures from 2008–2011 by broad commodity category and state/territory.

Broad commodity category	NSW	Vic	Qld	SA	WA	Tas	NT	ACT
Animal Products	19093	9619	10208	2723	3175	810	266	1291
Biologicals	420	350	230	58	107	25	8	13
Contaminated Goods/Footwear/Packaging	2411	1950	1033	471	926	122	41	141
Fruit – Fruit Products	4045	2787	1416	643	636	192	46	204
Grains, Legumes – Nuts	4827	3227	1795	751	983	216	50	260
Herbs – Spices	3303	2426	1526	627	618	268	64	166
Human Therapeutics	4931	5390	1968	787	995	258	70	236
Live Animals	52	46	19	8	13	5	0	4
Mushroom/Fungi	2035	1286	561	341	282	162	14	107
Plant/Plant Products	22816	19717	9192	4672	5502	1440	289	1156
Soil/Mineral Samples Fertiliser	405	333	160	82	98	25	8	19
Vegetable/Vegetable Products	2474	1430	680	320	391	109	19	122
Total	66924	49017	28819	11501	13764	3637	876	3728

NSW: New South Wales, Vic: Victoria, Qld: Queensland, SA: South Australia, WA: Western Australia, Tas: Tasmania, NT: Northern Territory, ACT: Australian Capital Territory.

field, averaged over the other fields, using overall measures of importance. These are a summary of impact of the splits based on each field. These values are only relative and have been standardised such that the largest value is set to 100. This gives an indication of the relative importance of each demographic field in the prediction of seizures, as compared with the relative importance values for the other demographic fields reported for the same model. Table 4 gives the relative importance values for the top 10 fields in a model based on all the available data. In each case the relationship was positive, with increasing seizure rate as the demographic field increased. Note that some language and ancestry fields have been deliberately obscured: Country A refers to an East Asian country for which Language A is the official language. These have been

Table 4. Top 10 relative variable importance measures.

Census field	Level	Variable importance
Equivalised Total Household Income	Nil income	100
Total Household Income	Nil income	91.8
Year of Arrival in Australia	2010	48.6
Country of Birth of Person	Country A	31.4
Educational Institution	Full time student aged 25+	27.1
Type of Educational Institution	University or other tertiary	20.6
Australian Citizenship	Not Australian	16.9
Ancestry 1st Response	Country A	14.9
Language Spoken at Home	Language A	14.5
Total Personal Income	Nil income	13.7

obscured in order to avoid potential labelling of social groups in society on the basis of race or ethnicity, gender, age etc. The point of the study was not to profile groups pejoratively, but to explore a method that can be used to assist in designing campaigns to raise awareness.

Overall, no household income, some relationship to Country A, recent arrival and university study dominate this list of important fields. These fields are also highly related, as international students are often recent arrivals from Country A without any household income. However, it is worth emphasising that the model did not consider counts of individuals with all of these characteristics at the SA2 level, only the counts of each within each SA2.

Given this relationship with students, it is worth considering the destinations of seizures in relation to universities. Figure 1 represents the seizure rates for each SA2 for the two capital cities with the most seizures, Sydney and Melbourne. In many cases the red hotspots are close to the locations of key university campuses.

As the units of study (SA2s) were spatially related, it is appropriate to comment on any spatial patterns observed. While considered in the model to assess spatial correlation, the longitude and latitude of the SA2 polygons did not feature highly in variable importance, with relative importance values of 0.4 and 0.2, respectively. This indicates that those SA2s with similar location did not, in fact, have similar seizures frequencies, after adjustment for demographic fields. A variogram of the residuals of the random forest model has been provided in the suppl. material 1 and also shows no evidence of spatial correlation.

This could be due, in part, to the spatial patterns in the seizure counts being strongly related to that of the predictors in the model, leaving no detectable residual spatial correlation. A simple linear regression analysis between seizure rate and the latitude and longitude of the SA2 indicated an association between seizure rates and longitude (but not latitude), suggesting this might be happening in part at least.

While the overall seizure rate is of primary concern, different kinds of seizures pose different kinds of risks and require different mitigation policies in response. As indicated in Tables 2 and 3, there are 12 broad commodity categories into which

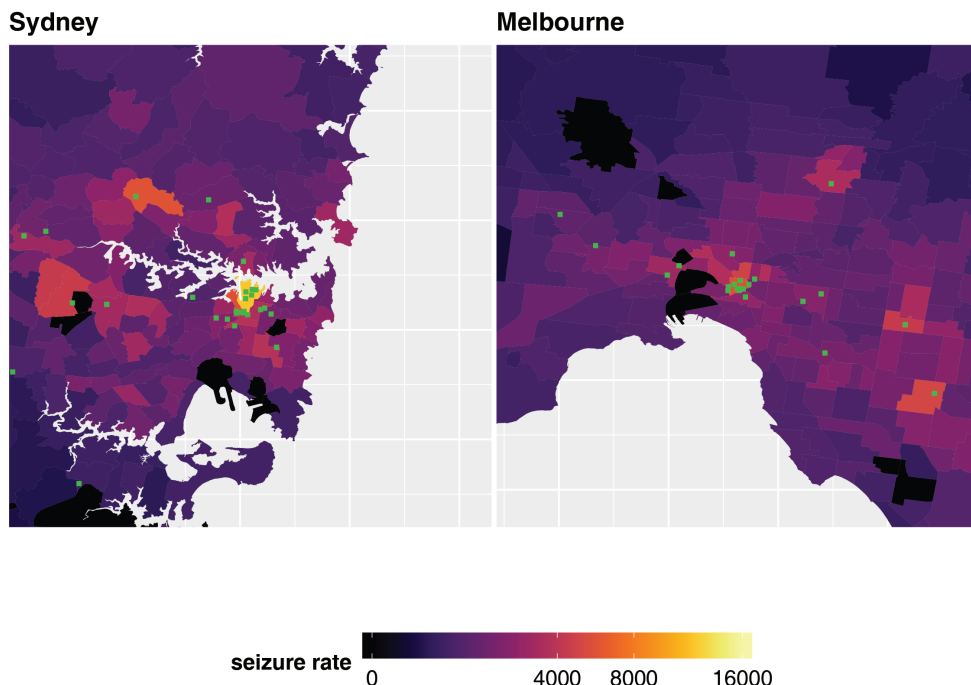


Figure 1. Seizure rate patterns by SA2 polygon for Sydney and Melbourne, per 100,000 people from 2008–2011. Green squares correspond to locations of university campuses.

seizures can be classed. Excluding live animals due to small counts, separate random forests were constructed for the seizures in each category, to compare the important demographic fields. The methods used were otherwise identical to those used for the analysis of the overall seizure rate, with the same relative variable importance measures available for interpretation.

Fields relating to no household income featured highly for all commodity categories, with university study and recent arrival also dominating most categories. East Asian Language A and/or some Country A ancestry were related to all the food categories (Fruit products, Legumes, Herbs, Mushrooms and Vegetable products), whereas another East Asian country was related to the destinations of animal products, an Eastern European ancestry and language were related to biologicals (this general class includes animal or microbial derived products such as foods, therapeutics, laboratory materials and vaccines) and language and ancestry from the Horn of Africa were related to human therapeutics. Seizures due to contaminated materials or soil/mineral samples were conspicuous for having no language or ancestry fields identified as important, which may be to do with the broad nature of these categories, with the biosecurity risk typically unrelated to the imported item itself and, instead, related to the presence of additional contaminants. Contamination, soil/mineral presence and plant products were all related to attendance of a university or other tertiary institution, with plant products also associated with those with high English language proficiency in particular.

Discussion

Our analysis provides insight into the spatial pattern of which, in the absence of border intervention, goods that present biosecurity risk may arrive in Australia. Each interception represents a measure of biosecurity risk averted. Our analysis suggests that there are population-level patterns in the demography of areas that receive a disproportionately high amount of biosecurity risk material by the international mail pathway. For example, SA2 regions with relatively high presence of university students who speak Language A at home are statistically closely related to high rate seizures of international mail articles. This insight suggests education campaigns might be used, for example, to provide information materials to relevant student groups at universities to better inform students about Australia's biosecurity imperatives or directed to particular suburbs of metropolitan areas which are more likely to receive risky goods. Future work, using independent data, could formally test the conjectured relationship between arrival counts and proximity to Universities.

The model described here can also be used to locate and profile particular demographic groups (and their usual residential locations) who are associated with a specific seized imported item. These education campaigns could therefore focus on the particular commodity types that this cohort are associated with, such as food-related importation information in Language A or human therapeutic information in the relevant African languages.

The usefulness of the results for providing information on policy and operational strategies is limited by the frequency with which the analysis can be repeated. While the biosecurity seizure data for international mail articles is continuously available for analysis, the Australian Census population data used in conjunction with mail seizure data is updated at 5-yearly intervals. If the length of time to complete tertiary education of the international student groups identified as high risk is less than 5 years, this means that educational campaigns such as distributing food related importation information would need to be directed towards new cohorts of students who meet the demographic profiles identified in this analysis, as well as current students. The demographic characteristics of the population may change over the 5-yearly interval, although such changes tend to be over a longer period. This change would limit the usefulness of the profiles for deciding where and to whom information about importing particular commodity types should be provided.

Well-directed information campaigns would have the potential to increase awareness and understanding of Australia's biosecurity importation rules and the reasons for them, amongst those who may inadvertently import biosecurity risk material. However, information on its own is unlikely to affect any deliberate, criminal importation activity. As well as providing a focus for educational campaigns, this analysis could also provide information about operational strategies that could target incoming international mail for inspection at the major points of entry. For example, the department is using a number of strategies for biosecurity compliance and inspection in the mail pathway, including working with

other agencies to improve screening and sampling techniques to intercept high-risk materials in international mail based on profiling information (Department of Agriculture 2016b). The analysis in this study has provided information about some of these strategies.

There is also an encouraging finding in relation to biosecurity risk: there was no evidence that these materials were destined for areas with greater agricultural land use generally, nor greater employment in such industries, as neither agricultural land use nor employment featured high in the list of variable importance.

These results also indicate there is considerable utility obtained from the use of the random forests model, which can be used to predict seizures of biosecurity material in international mail for a given situation. That is, given a set of demographic characteristics, the random forests model can be used to estimate the likely number of mail seizures for a specific imported product.

A shortcoming of the analysis is the lack of information available concerning the rate at which mail articles arrive at each SA2 polygon. Hence, the higher count of seized articles for specific polygons could be due in part to a higher volume of mail. However, this is not a particularly important caveat from the policy point of view, where the magnitude of biosecurity risk material is the primary apprehension. A further shortcoming is that we have no way of knowing from the mail interception records whether an inspection was random or targeted. Therefore there is no design-based guarantee of unbiased parameter estimates. The interpretation of the results should take this caveat into account.

Finally, it is in the nature of a geographical analysis, such as that outlined in this paper, that mail items that are posted to fake addresses could not be considered in the analysis. Unfortunately, the technique of using a fraudulent address is known anecdotally within the Department to be associated with a greater risk of deliberate, criminal importation. However, there already exist department procedures to monitor and analyse mail of this kind. This nature of risk is different from the kind of importation behaviour that can be targeted with the campaigns that would be motivated by this analysis.

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Supplementary material I

Variogram of the residuals of the random forest model

Authors: Sandy Clarke, Nyree Stenekes, Robert Kancans, Chris Woodland, Andrew Robinson

Data type: statistical data

Explanation note: A variogram designed to visually assess whether there is spatial correlation present in the residuals of the random forest model. This does not indicate any spatial correlation.

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Environmental harshness drives spatial heterogeneity in biotic resistance

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Abstract

Ecological communities often exhibit greater resistance to biological invasions when these communities consist of species that are not closely related. The effective size of this resistance, however, varies geographically. Here we investigate the drivers of this heterogeneity in the context of known contributions of native trees to the resistance of forests in the eastern United States of America to plant invasions. Using 42,626 spatially referenced forest community observations, we quantified spatial heterogeneity in relationships between evolutionary relatedness amongst native trees and both invasive plant species richness and cover. We then modelled the variability amongst the 91 ecological sections of our study area in the slopes of these relationships in response to three factors known to affect invasion and evolutionary relationships – environmental harshness (as estimated via tree height), relative tree density and environmental variability. Invasive species richness and cover declined in plots having less evolutionarily related native trees. The degree to which they did, however, varied considerably amongst ecological sections. This variability was explained by an ecological section's mean maximum tree height and, to a lesser degree, SD in maximum tree height ($R^2_{GLMM} = 0.47$ to 0.63). In general, less evolutionarily related native tree communities better resisted overall plant invasions in less harsh forests and in forests where the degree of harshness was more homogenous. These findings can guide future investigations aimed at identifying the mechanisms by which evolutionary relatedness of native species affects exotic species invasions and the environmental conditions under which these effects are most pronounced.

Keywords

Environmental harshness, environmental variability, evolutionary divergence, forests, invasive plants, phylogeny, relative tree density

Introduction

Observations across large geographic areas reveal considerable spatial heterogeneity in the degree to which ecological communities are invaded by non-native species (Stohlgren et al. 2006, Liebhold et al. 2013, Iannone et al. 2015). Spatial variability in the degree to which various ecological factors affect invasions partially explains this heterogeneity (e.g. Riitters et al. 2018). Identifying what drives this heterogeneity is of importance to both basic ecological understanding and land management aimed at controlling invasive species. Analyses of increasingly available large-scale forest data have revealed that forests exhibit large-scale spatial heterogeneity in both the number and dominance of invasive plant species that are present within them (Iannone et al. 2015, Oswalt et al. 2016). Understanding what causes this heterogeneity will improve basic understanding of forest plant invasions and help to protect the many ecosystem services that forests provide from threats posed by invasive plants (Gonzalez et al. 2005, Martin et al. 2009, Pejchar and Mooney 2009).

Analyses of the same large-scale forest data have also revealed evidence that native tree communities contribute to the ability of forests to resist plant invasions in general, i.e. regardless of invader growth form, and that these contributions vary spatially (Guo et al. 2015, Iannone et al. 2016). The characteristics of native tree communities most negatively related to plant invasions (i.e. invasive plant species richness and dominance) include aboveground native tree biomass and the degree to which native tree species are evolutionarily related (Iannone et al. 2016). The detected contribution of native tree biomass to invasion resistance likely reflects the fact that trees are a leading component of forest biomass, primary productivity and resource uptake (Muller 2003). The contribution of evolutionary relatedness of native trees to invasion resistance likely reflects the assumption that communities containing less evolutionarily related species exhibit greater diversity in both measurable functional traits and unidentified phenotypic traits and, thus, a greater breadth in niche usage (Faith 1992, Webb et al. 2002, Lososová et al. 2015, Tan et al. 2015, but see Gerhold et al. 2015).

The objective of this investigation was to determine the degree to which environmental characteristics of forests drive spatial heterogeneity in the effects that native tree evolutionary relatedness has on overall forest plant invasions. This investigation was conducted in the forests of the eastern United States of America (USA). We pursue this objective in the context of three separate characteristics of evolutionary relatedness: how divergent (*sensu* Tucker et al. 2017) species are relative to one another across a phylogenetic tree (i.e. phylogenetic species clustering [PSC] and phylogenetic species variability [PSV]; [Helmus et al. 2007]), the amount of evolutionary history contained

within these phylogenetic relationships (i.e. phylogenetic diversity [PD]; [Faith 1992]) and the evenness in abundance at which species occur across a phylogenetic tree (i.e. phylogenetic species evenness [PSE]; [Helmus et al. 2007]). Regarding environmental characteristics, we investigate environmental harshness, as defined by Marks et al. (2016) and relative tree density, both of which can affect the establishment and growth of invasive plants (Theoharides and Dukes 2007, Guo et al. 2015). We also investigate the role of environmental variability, as it can accelerate evolutionary radiation amongst native species via allopatric speciation (Qian and Ricklefs 2000) and can reflect niche availability for invasions (Davies et al. 2005).

Methods

Evolutionary relatedness and biotic resistance

Evolutionary relatedness is typically defined within the context of phylogenetic relatedness or the locations of species relative to one another across a phylogenetic tree that describes the hypothesised evolutionary relationships amongst species. Many studies investigating the effects of phylogenetic relatedness on invasion have done so in the context of the evolutionary relatedness between invasive and native species, i.e. within the context of “Darwin’s naturalisation hypothesis” that species from novel genera may have an advantage when invading new locations because they are less likely to compete with closely related species or share natural enemies with them (e.g. Diez et al. 2008, Lososová et al. 2015). Nevertheless, we are unlikely to know ahead of time the particular species that will invade a given community. For this reason, knowing how the phylogenetic relatedness amongst native species in a given community affects invasion in general is likely of greater utility in understanding spatial heterogeneity in the degree to which native ecosystems resists plant invasions. Ecological communities consisting of species that are more divergent relative to one another across the phylogenetic tree of life can exhibit greater resistance to invasion (Gerhold et al. 2011, Lososová et al. 2015), although the degree of resistance varies considerably across large spatial scales (Iannone et al. 2016). This geographic variability suggests that the effect of evolutionary relatedness of native communities on exotic invasions is itself affected by other factors.

Data compilation

To meet our objective, we first obtained native tree and invasive plant data from 42,626 forested plots from the United States Department of Agriculture’s Forest Inventory and Analysis programme (FIA) located within the two ecological domains (*sensu* Cleland et al. 1997) of the eastern USA (Suppl. material 1, fig. S1.1). The location of these data, as well as all other data used for subsequent analyses in this paper can be found below in the paper’s Data accessibility section. FIA monitors spatiotemporal patterns of for-

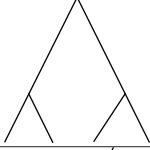
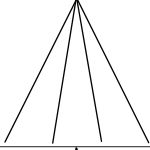
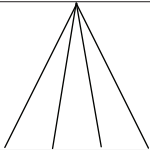
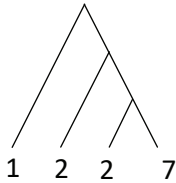
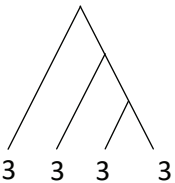
est conditions at the national-level using a fixed grid of permanent plots occurring at an approximate intensity of one plot for every 2,428 ha of forests; all plots are 0.40 ha in size and are defined using a consistent plot design (Bechtold and Patterson 2005). Forests are defined as areas at least 36.6 m wide and 0.40 ha in size that historically or currently have at least 10% tree cover (for trees of any size).

We used four metrics (Table 1) to estimate three characteristics of evolutionary relatedness amongst the native trees in each plot. First, we constructed a phylogenetic supertree of 397 native angiosperm and gymnosperm tree species occurring in the FIA plots of the contiguous 48 states (Potter 2018). This reference phylogeny, with branch lengths measured in millions of years, was constructed based on a review of 189 molecular systematics and paleobotanical studies. Using this phylogenetic tree and the R package Picante (Kembel et al. 2010), we quantified two different aspects of phylogenetic divergence, following Helmus et al. (2007) —phylogenetic species variability (PSV) and phylogenetic species clustering (PSC). PSV quantifies variability amongst species in a hypothetical random (non-selected) trait, thus quantifying how divergent species are relative to one another across an entire phylogenetic tree and the extent to which the phylogenetic arrangement of these species represents a star phylogeny, as illustrated in Table 1. PSC quantifies the degree to which the phylogenetic branch tips for species in a given community are divergent, or clustered, relative to one another. From the same phylogenetic tree, we also estimated the amount of evolutionary history within each plot using the metric phylogenetic diversity (PD) proposed by Faith (1992). PD is estimated by summing the lengths of the phylogenetic branches for the tree species found within a given plot. By definition, PD increases with species richness. The utility of PD in describing the amount of evolutionary history within a given community was also confirmed by Tucker et al. (2017). Lastly, we calculated the phylogenetic species evenness (PSE) metric proposed by Helmus et al. (2007). This metric is an indicator of phylogenetic divergence that accounts for the relative abundances of species within the investigated community. PSE equals PSV when all species are equally abundant in a community and declines as they are decreasingly so.

A benefit of using PSV, PSC and PSE is that these metrics of phylogenetic divergence do not require prior knowledge of the regional species pool from which species could populate a plot (Helmus et al. 2007). An initial correlation analysis revealed PD to be strongly related to and, thus, dependent on, the number of native tree species in each plot ($r_{PD} = 0.82$). The three other phylogenetic metrics, however, exhibited weaker relationships with native tree species richness ($r_{PSV} = -0.31$, $r_{PSC} = 0.49$ and $r_{PSE} = 0.09$) and, thus, reflected more independent characteristics.

We assessed overall plant invasion in each plot by compiling data on invasive plant richness and cover data, following Iannone et al. (2016). Invasive richness is the number of invasive plant species found and invasive cover is the summed total cover of these species (which can exceed 100% of the area of a plot because of overlap by individual plants). Invasive richness and cover serve as indicators of invasive species establishment and dominance, respectively. FIA defines invasive plants in accordance with USA Executive Order 13112 as non-native plant species likely to cause economic

Table 1. Explanation of the four investigated metrics of evolutionary relatedness. PD is defined by Faith (1992) and PSE, PSV and PSC are defined by Helmus et al. (2007).

Metric	Definition of metrics & notes	Lower	Higher
Phylogenetic species clustering (PSC)	Quantifies the degree to which phylogenetic branch tips are divergent or clustered relative to one another. Ranges from 0 (low divergence) to 1 (high divergence)		
Phylogenetic species variability (PSV)	Quantifies variability amongst species in a hypothetical neutral trait and thus divergence across the branch lengths of a phylogeny. Ranges from 0 (low) to 1 (high, star phylogeny)		
Phylogenetic diversity (PD)	Summed lengths of phylogenetic branches. Values increase with species richness. Positive value has no upper limit. Increases with greater values		
Phylogenetic species evenness (PSE)	Hypothesised to reflect evenness in traits and phenotypic variation. PSE = PSV when all species are equally abundant and declines with greater differences in abundance. NOTE: Numbers at branch tips on the right signify number of individuals	 1 2 2 7	 3 3 3 3 PSE = PSV

or environmental harm (Ries et al. 2004). The list of monitored invasive plants in the eastern USA includes approximately 76 different species; some species were merged into single groups to accommodate field identification. These species include 18 forbs, 9 grasses, 21 shrubs, 14 trees and 14 vines (Suppl. material 2, table S2.1). Although invasive plant sampling protocols, including the specific species monitored, vary between the Northern and Southern FIA Administrative Regions (described in Suppl. material 2, text S2.1), this variability has little effect on macroscale invasion patterns (Iannone et al. 2015). Furthermore, most of the invasive plants monitored are of concern to large portions of each and, in some cases both, of the administrative regions, alleviating concerns about spatial variability in invasive plant species pools.

Confirming/quantifying spatial variability in invasion resistance

Using a mixed-effects modelling framework developed by Dixon Hamil et al. (2016), we modelled invasive richness and cover in response to the four phylogenetic metrics (PSC, PSV, PSE and PD), allowing for independent (i.e. random) intercept and slope estimates for each of the 91 ecological sections (*sensu* Cleland et al. 1997) nested within our study region (Suppl. material 1, fig. S1.2). Phylogenetic metrics were stand-

ardised $[x - \text{mean}(x)/\text{SD}(x)]$, allowing for cross-variable comparison (Schielzeth 2010). Inspection of variance inflation factors (Legendre and Legendre 2012) revealed no evidence of complications due to collinearity. We assessed model fit using the coefficient of determination for generalised mixed-effect models, i.e. R^2_{GLMM} (Johnson 2014). To assess statistical significance, we resampled section-level slope estimates (i.e. conditional plus fixed estimates) 10,000 times allowing for replacement and calculated the bias corrected, accelerated 95% confidence interval (CI) of each bootstrapped distribution (Efron and Tibshirani 1986). We assumed the phylogenetic metric to be a statistically significant indicator of biotic resistance across our study region when its 95% CI encompassed values less than zero. Likewise, we assumed a phylogenetic metric to be an indicator of invasion success when its 95% CI encompassed values greater than zero. We relied on bootstrapped rather than actual distributions to estimate 95% CIs because actual distributions were non-normal (Suppl. material 3, fig. S3.1).

Identifying drivers of spatial heterogeneity in invasion resistance

We compiled data from the FIA database on plot-level maximum tree height (m) and relative tree density. Maximum tree height was used as an inverse indicator of environmental harshness. Marks et al. (2016) found maximum tree height to be negatively correlated to multiple environmental indicators of environmental harshness across forests of both the eastern and western USA. Relative tree density was calculated as described by Potter and Woodall (2014). This standardised metric quantifies the number of trees per unit area currently in a given FIA plot and divides that value by the maximum number of trees that could grow in that plot. We then calculated means and SD for each of these metrics at the ecological section level (Suppl. material 1, fig. S1.2; Suppl. material 1, table S1.1). Means estimated overall section-level environmental harshness and relative tree density, while SD of these metrics served as section-level indicators of the environmental (abiotic and biotic) variability experienced by invading plants. As an additional, indirect metric of environmental variability, we calculated the mean Jaccard's distance (based on absence/presences of native tree species) amongst plots within each of the 91 ecological sections. Ecological sections having greater mean Jaccard's distances in native tree species composition were assumed to be more environmentally variable.

We conducted preliminary regression analyses to assess the degree to which maximum tree height, relative tree density and SD in these variables predicted forest age. We did so to rule out the possibility of our findings reflecting nothing more than forest successional stages, i.e. variation between young and old forests in the degree of invasion. Both maximum tree height and relative tree density explained relatively small proportions of variability in FIA estimates of forest stand age at both the individual plot and ecological section levels (range in $R^2 = 0.04$ to 0.24). SD of maximum tree height and relative density also explained relatively small proportions of forest stand age ($R^2 = 0.25$ and 0.04 , respectively). These low R^2 values revealed that mean and SD

of maximum tree height and relative density were largely indicative of environmental conditions other than forest successional stages.

We modelled slope estimates for relationships between phylogenetic metrics indicative of biotic resistance and invasive richness and cover in each of the 91 ecological sections (determined as described above) in response to the section-level mean and SD of maximum tree height and relative tree density, as well as section-level estimates of mean Jaccard's distance (model shown in Table 2). We used these statistical models to assess whether environmental harshness, relative tree density and/or environmental variability drive spatial heterogeneity in the degree to which evolutionary relatedness contributes to invasion resistance. We assessed model fit using the conditional estimate for the coefficient of determination for generalised mixed-effect models, i.e. R^2_{GLMM} (Johnson 2014).

Prior to analysis, we standardised explanatory variables [$x - \text{mean}(x)/\text{SD}(x)$], allowing us to assess the relative contribution of each to this spatial heterogeneity (Schiegg 2010). To account for possible spatial autocorrelation amongst more closely located ecological sections, we incorporated the ecological province (Suppl. material 1, fig. S1.3), i.e. the larger ecoregion scale in which each ecological section was nested, into statistical models as a random effect. The distribution of slope estimates for relationships between invasion and phylogenetic metrics were left-skewed (Suppl. material 3, fig. S3.1). To address this, we transposed slope estimates to positive values greater than 1 and transformed the data using a power transformation [$(x + \text{abs}(\min(x)) + 1)^7$] to help meet the assumption of normality. Inspection of variance inflation factors (Legendre and Legendre 2012) revealed no evidence of complications due to collinearity.

Statistical analyses were conducted in R v 3.0.1 (R Core Team 2014) using the nlme package (Pinheiro et al. 2017) to construct linear mixed-effects models, the MuMIn package (Bartoń 2014) to estimate coefficients of determination and the bootstrap package (Tibshirani and Leisch 2013) to conduct bootstrap analyses.

Results

Spatial heterogeneity in invasion resistance

Mapping the section level slope estimates determined via mixed-effects modelling confirmed spatial variability in relationships between phylogenetic (PSC, PSV, PD and PSE) and invasion (richness and cover) metrics (Fig. 1). Slope values for PSC and PSV were largely negative across ecological sections, while those for PD and PSE were largely positive. The 95% confidence intervals (CI) of the bootstrapped distributions of section-level slope estimates revealed these trends to be statistically significant, i.e. 95% CIs did not encompass zero (Suppl. material 3, fig. S3.2). Slope values for PSC and PSV also exhibited greater spatial variability and magnitudes in their relationships with invasive richness and cover than did PD and PSE (Fig. 1;

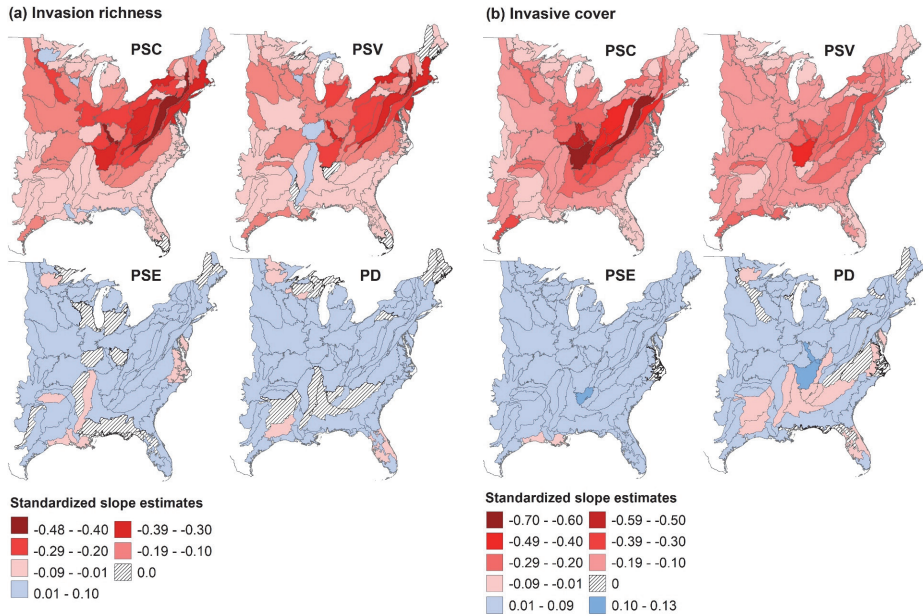


Figure 1. Standardised relationships between four metrics of evolutionary relatedness and invasive (a) richness and (b) cover.

Suppl. material 3, fig. S3.2). (See Suppl. material 3, table S3.1 for values of section level slope estimates.) Given that PD and PSE were not indicative of biotic resistance to invasion, we did not investigate the drivers of spatial heterogeneity in relationships between these metrics and invasion metrics.

Drivers of spatial heterogeneity in biotic resistance to invader establishment (i.e. invasive richness)

Spatial variability in the degree to which both PSC and PSV were related to invasive richness was largely explained by mean and SD maximum tree height (Table 2; R^2_{GLMM} of statistical models = 0.55 and 0.47, respectively). Slopes of all other model terms were not statistically significant from zero (p -values = 0.15 to 0.57). Slopes for mean maximum tree height were negative (Table 2), revealing both PSC and PSV to be more negatively related to invasive richness in ecological sections having greater maximum tree heights (Figs 2a, c). In contrast, slopes for SD maximum tree height were positive (Table 2). This reveals both PSC and PSV to be less negatively related to invasive richness in ecological sections having more variable maximum tree heights (Figs 2b, d). Standardised slope estimates revealed mean maximum tree height to have more than twice the effect as SD on this spatial variability for PSC and a 27% greater effect than

Table 2. Results of linear mixed-effects models. These models were used to determine the relative contribution of mean and SD of maximum tree height and relative tree density, as well as mean Jaccard’s distance, to spatial heterogeneity in relationships between metrics of phylogenetic divergence (PSC and PSV) and invasion (invasive richness and cover). Models contained ecological provinces as a random effect.

Dependent variable	Explanatory variables					
Section-level	Mean Max	SD Max	Mean	SD	Mean	R^2_{GLMM}
slope estimates for:	tree ht.	tree ht.	Rel. density	Rel. density	Jaccard’s dist.	
Invasive richness ~ PSC	$-2.66 \pm 0.54^{****}$	$1.29 \pm 0.55^*$	0.83 ± 0.60	-0.24 ± 0.42	-0.73 ± 0.50	0.55
Invasive richness ~ PSV	$-2.18 \pm 0.59^{***}$	$1.71 \pm 0.60^{**}$	0.86 ± 0.66	-0.55 ± 0.46	-0.75 ± 0.55	0.47
Invasive cover ~ PSC	$-6.64 \pm 1.17^{****}$	0.07 ± 1.19	1.94 ± 1.31	0.62 ± 0.91	-0.21 ± 1.09	0.63
Invasive cover ~ PSV	$-1.18 \pm 0.29^{***}$	0.16 ± 0.29	0.37 ± 0.32	0.04 ± 0.22	-0.08 ± 0.27	0.49

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; **** $p < 0.0001$

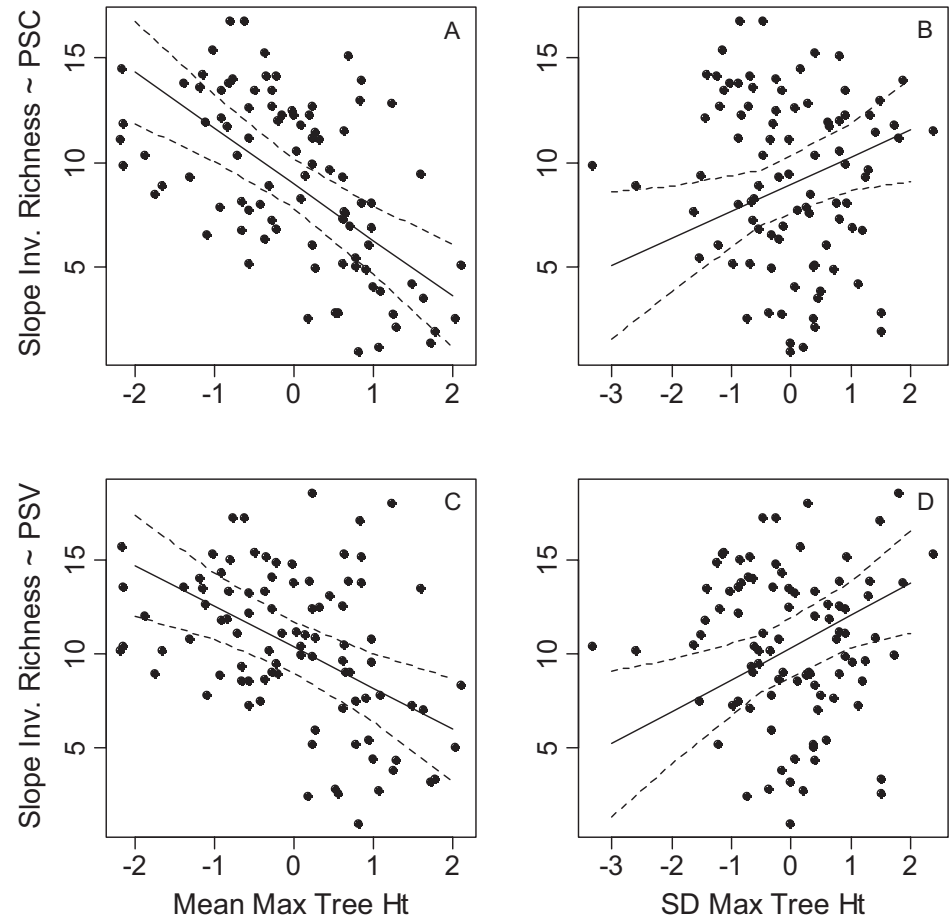


Figure 2. Effects of mean and SD maximum tree height in 91 ecological sections on the degree to which PSC (A,B) and PSV (C,D) affect invasive species richness (i.e. slope values for these relationships). Note that values on x and y axes were transformed (z-transformed and $[(x + \text{abs}(\min(x)) + 1)^7]$, respectively) prior to analysis. Untransformed values for slopes were largely negative (Fig. 1; Suppl. material 3, fig. S3.1).

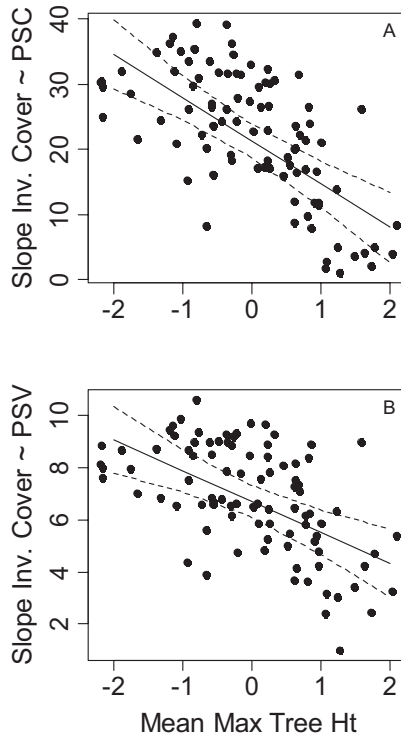


Figure 3. Effects of mean maximum tree height in 91 ecological sections on the degree to which PSC (A) and PSV (B) affect invasive species cover (i.e. slope values for these relationships). Note that values on x and y axes were transformed (z-transformed and $[(x + \text{abs}(\min(x)) + 1)^7]$, respectively) prior to analysis. Untransformed values for slopes were largely negative (Fig. 1; Suppl. material 3, fig. S3.1)

SD for PSV (Table 2). Slopes for mean maximum tree height had smaller p -values (Table 2) and smaller 95% CIs relative to their slopes (Fig. 2), than those for SD maximum tree height, suggesting a more consistent impact on spatial heterogeneity in relationships between invasion richness and both PSC and PSV.

Drivers of spatial heterogeneity in biotic resistance to invader dominance (i.e. invasive cover)

Spatial variability in the degree to which both PSC and PSV were related to invasive cover was explained solely by mean maximum tree height (Table 2; R^2_{GLMM} of statistical models = 0.63 and 0.49, respectively). Slopes of all other model terms were not statistically significant from zero (p -values = 0.26 to 0.95). Slopes for mean maximum tree height were negative (Table 2), revealing both PSC and PSV to be more negatively related to invasive cover in ecological sections having greater overall maximum tree heights (Figs 3a, b).

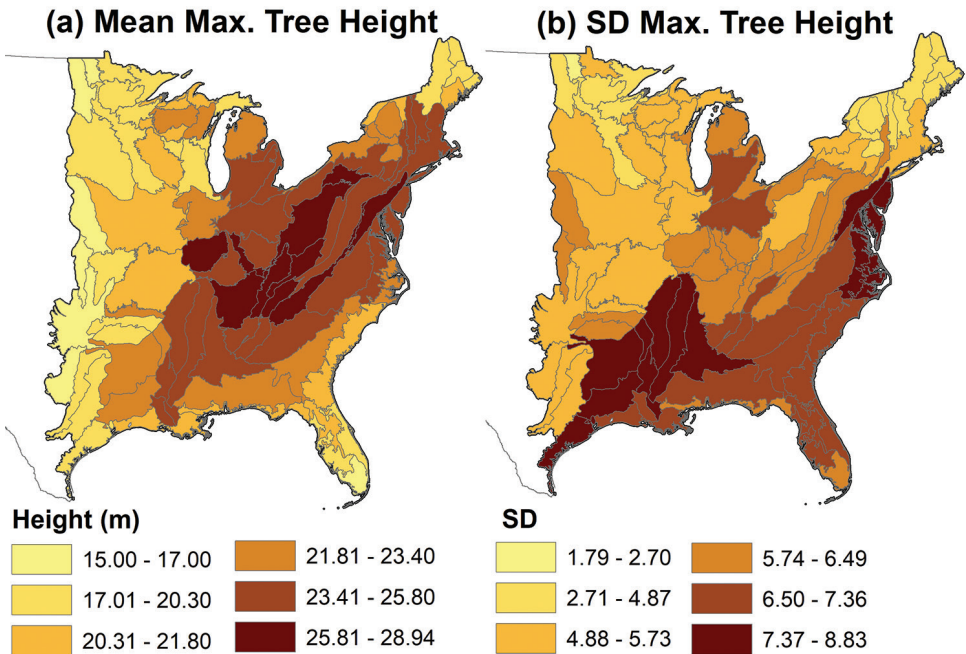


Figure 4. Section level means (a) and SD (b) for maximum tree height (i.e. an inverse metric of environmental harshness).

Spatial context

Follow-up mapping of section-level estimates of statistically significant explanatory variables shown in Table 2, i.e. mean and SD of maximum tree height, revealed spatial patterns contributing to our current findings. The greatest values for mean maximum tree height occurred in and around the Appalachian Mountains (Fig. 4a) where both PSC and PSV exhibited stronger negative associations with invasive richness and cover (Fig. 1). This pattern contributed to the strong negative slope values exhibited by maximum tree height in all statistical models (Table 2). The greatest values for SD of maximum tree height occurred in the southern portion of our study region (Fig. 4b) where PSC and PSV both tended to exhibit weaker and sometimes positive relationships with invasive richness (Fig. 1). This pattern contributed to the positive slope values for SD maximum tree height in statistical models for relationships between invasive richness and both PSC and PSV (Table 2).

Discussion

We found evidence that environmental harshness and, to a lesser degree, variability in environmental harshness drive spatial heterogeneity in the contribution of phylogenetic divergence (PSC and PSV) of native trees to biotic resistance to overall plant

invasions in eastern USA forests. While spatial heterogeneity in the contribution of native trees to biotic resistance to forest plant invasions was previously noted (Iannone et al. 2016), this investigation is the first to our knowledge that identifies potential drivers of this large-scale heterogeneity. This detected contribution of phylogenetic divergence to invasion resistance illustrates how variation in localised processes by which evolutionary relatedness is hypothesised to limit invasions, e.g. niche overlap/competitive exclusion (Procheş et al. 2008, Thuiller et al. 2010), can contribute to complex large-scale invasion patterns. In addition, the spatial heterogeneity revealed also illustrates the utility of applying a community-level framework when investigating large-scale invasion patterns (Shea and Chesson 2002). Finally, our findings support the value of considering biotic and environmental filters to invasion in unison in order to understand overall invasion patterns (Pearson et al. 2018).

In contrast to phylogenetic divergence, we found no evidence that the amount of evolutionary history (i.e. PD) or the evenness at which these native tree species occur across a given community's phylogenetic tree (i.e. PSE) contribute to biotic resistance across macroscales. The consistently positive associations that PD and PSE shared with both invasive richness and cover suggests these metrics to be more indicative of niche availability than biotic resistance, at least at the spatial scale of our investigation. The weak magnitudes of these associations also revealed them to be of little value in predicting macroscale invasion patterns. The positive association between PD and invasion was not surprising, as this metric is strongly related to native species richness, which itself is positively related to invasive richness and cover at large spatial scales (Stohlgren et al. 2006, Fridley et al. 2007, Iannone et al. 2016). Causes of the positive association between phylogenetic species evenness (PSE) and invasion are less clear. Even though species evenness can contribute to biotic resistance at small spatial scales in grasslands (Wilsey and Polley 2002), this tells us little about how species evenness affects large-scale invasions in forests. Thus, studies to determine how variability in spatial scale and ecosystem type affects the contribution of species evenness to biotic resistance are needed.

By revealing factors that affect the strength of relationships between phylogenetic divergence and invasion, our study revealed conditions under which phylogenetic divergence of native tree communities likely contributes most to invasion resistance in forest ecosystems. Standardised slope estimates revealed that mean maximum tree height was the explanatory variable having the greatest effect. This factor was negatively correlated with slope values for relationships between both PSC and PSV and both invasion richness and cover. Given that maximum tree height is an inverse measure of environmental harshness (Marks et al. 2016), these negative relationships reveal a greater potential for more phylogenetically divergent tree communities to limit invader establishment and dominance under less harsh environmental conditions. This effect may reflect the long-recognised decline in the ecological importance of competition in more harsh environments (Bertness and Callaway 1994). That is, an invader's ability to deal with stress may be more important than its ability to deal with competition

when invading harsher environments, regardless of the niche space occupied by the native community. Determining the component(s) of environmental harshness that most affect relationships between phylogenetic relatedness and invasion will increase our understanding of the causes of the patterns revealed here. Investigating factors both related to tree height and that directly affect plant growth, e.g. soil productivity, drought, cold etc. (Marks et al. 2016), may be fruitful.

Increased environmental variability across large geographic areas can increase species richness (Qian and Ricklefs 2000), which, in some situations, is positively related to certain metrics of evolutionary relatedness (Potter and Woodall 2014). Increased environmental variability is also positively associated with invasions (Davies et al. 2005). For these reasons, we expected factors indicative of environmental variability to affect the magnitude of relationships between metrics of phylogenetic divergence and invasion. We found such evidence for the SD of maximum tree height, but not for SD of relative tree density or mean Jaccard's distances. The positive correlation of SD of maximum tree height to slope values for relationships between invasive richness and both PSC and PSV reveals phylogenetically divergent tree communities to limit invader establishment more in ecological sections that are less variable regarding environmental harshness. However, smaller slope and larger *p*-value estimates for SD vs. mean maximum tree height reveal overall environmental harshness to be more influential.

The decline in the effects of phylogenetic divergence on invasion in ecological sections having more variable maximum tree height may reflect an increased number of locations having more harsh environments. That is, it indicates an increase in the number of locations where phylogenetic divergence affects invader establishment less. An increase in the number of locations experiencing canopy disturbance (natural or human) may also contribute to our finding regarding SD in maximum tree height given that increased light facilitates forest plant invasions (Eschtruth and Battles 2009, Iannone et al. 2013). However, given that SD in maximum tree height and mean stand age are only weakly related, it is likely that increased SD in maximum tree height reflects more than increased rates of canopy disturbance. Declines in the effects of phylogenetic divergence on invasion in ecological sections having more variable maximum tree height may also reflect the previously noted positive associations between invasion and environmental variability (Davies et al. 2005). Considering components of forest plant communities other than, or in addition to, native trees, e.g. native understorey plants, soils etc., is likely to improve understanding of how environmental variability affects large-scale forest plant invasions.

We utilised two different measures of invasion — invasive species richness and cover — as both provide different perspectives on invasion patterns. Invasive richness is an indicator of invader establishment and invasive cover is an indicator of invader dominance. Prior theoretical and empirical investigations reveal the deeper understanding that can be gained by considering multiple invasion metrics simultaneously within the same investigation (Kennedy et al. 2002, Stohlgren et al. 2003, Guo and Symstad 2008, Catford et al. 2012, Iannone et al. 2015). For instance, we found evi-

dence that the effects of phylogenetic divergence on both invader establishment and dominance (i.e. richness and cover, respectively) declines with increased environmental harshness. In contrast, variability in environmental harshness only influenced the ability of phylogenetic divergence to affect invasive plant establishment and not invasive plant dominance. Based on our findings, we would predict that, even if phylogenetic divergence does not prevent invader establishment in a given area due to that area exhibiting greater spatial variability in environmental harshness, it might still limit invader dominance so long as the overall/mean environmental harshness of the area is low. This insight is of practical importance given that invasive cover may reflect invader impacts more than invasive species richness, potentially making it of greater relevance to invasive plant management (Guo and Symstad 2008, Hillebrand et al. 2008).

Identifying the factors that affect the ability of PSC and PSV to contribute to invasion resistance may also help to reveal how characteristics of evolutionary relationships (e.g. divergence, branch lengths and species evenness) emerge under different environmental conditions. For instance, both PSC and PSV limit invader establishment (as estimated by invasive richness) to greater degrees in forests that are less harsh. Therefore, the levels of environmental harshness found in a forest, by indirectly affecting invader establishment, have the potential to affect future PSC and PSV values for that forest. Therefore, our findings illustrate how knowing the phylogenetic relationships within an ecological community can help to understand the conditions from which these relationships emerge, i.e. the “phylogenetic-patterns-as-results utility” of known phylogenetic relationships (Gerhold et al. 2015).

Conclusions

We found evidence that environmental harshness and, to a lesser degree, spatial variability in environmental harshness, affect the ability of more phylogenetically divergent native tree communities to limit the establishment and dominance of invasive plants. Therefore, through indirect pathways, these factors may affect short-term invasion patterns and community-level change and, in so doing, affect the long-term characteristics of evolutionary relationships. Nevertheless, these factors did not explain all variability in phylogenetic-invasion relationships. Therefore, future investigations are needed. Considering how other known drivers of invasion patterns, such as propagule pressure and plant functional traits, as well as understorey native plant communities and forest soils, contribute to variability in the degree to which phylogenetic divergence of native trees contributes to invasion resistance, will likely be beneficial. Also needed is the determination of the component(s) of environmental harshness most contributing to our findings and the mechanisms by which phylogenetic divergence amongst native trees affects overall plant invasion. Controlled experiments replicated across our study region would greatly help in this regard. Such considerations will increase our understanding of how the evolutionary relatedness amongst species in a given community affects invasions and community change.

Data accessibility

Iannone BV III, Potter KM, Guo Q, Jo I, Oswalt CM, Fei S (2018) Data on native tree diversity (species richness and phylogenetic), biomass, relative density, tree height and invasive plants in forests of the eastern USA. Purdue University Research Repository. <https://purr.purdue.edu/publications/3072/1> doi: 10.4231/R7GX48TW.

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Supplementary material 1

Locations of Northern and Southern FIA Regions and of the ecological domains, provinces and sections in which study plots were located

Authors: Basil V. Iannone III, Kevin M. Potter, Qinfeng Guo, Insu Jo, Christopher M. Oswalt, Songlin Fei

Data type: occurrence

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Link: <https://doi.org/10.3897/neobiota.40.28558.suppl1>

Supplementary material 2

Description of differences between Northern and Southern FIA Regions in invasive plant species monitoring protocols

Authors: Basil V. Iannone III, Kevin M. Potter, Qinfeng Guo, Insu Jo, Christopher M. Oswalt, Songlin Fei

Data type: protocols

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Supplementary material 3

Section-level standardised slope estimates for the 91 ecological sections from initial models of invasive richness and cover in response to four metrics of evolutionary relatedness—PSC, PSV, PD and PSE

Authors: Basil V. Iannone III, Kevin M. Potter, Qinfeng Guo, Insu Jo, Christopher M. Oswalt, Songlin Fei

Data type: supporting data

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