

META-ANALYSIS



A global synthesis of the effects of biological invasions on greenhouse gas emissions

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ABSTRACT

Aim Evidence is mounting that biological invasions profoundly alter the capacity of ecosystems to regulate or mitigate greenhouse gas (GHG) emissions – a crucial ecosystem service in a changing climate. However, the growing literature has revealed different, even contradictory results and the general pattern over large spatial scales remains obscure. This study synthesizes the effects of invasions by different alien taxa on major GHG emissions.

Location Global.

Methods A structured meta-analysis of 68 case studies was performed to determine the generality of the effects of biological invasions on emissions of three GHGs and assess the extent to which the heterogeneity of effects can be explained by recipient ecosystems, invasive taxa, functional traits, climate and methodological aspects.

Results Invasive alien species increased N₂O emissions but promoted carbon sequestration. Effects on CH₄ emissions remained inconclusive. Given the general trends, effects differed by ecosystems, with greater N₂O emissions in invaded forest and higher increase in carbon stock in invaded grassland. Invasive taxa also mediated the effects of invasions: invasive plants enhanced carbon storage whereas animal invaders consistently showed negative effects. Focusing on exotic plant invasions, N-fixing species caused greater N₂O emissions than non-N-fixing species, and for carbon stock, N-fixing and woody plants exerted stronger positive effects than non-N-fixing and herbaceous plants, respectively. Moreover, climatic factors explained the variation in effects of exotic plant invasions but not those of animal invasions. The effects of plant invasions on carbon content varied nonlinearly with climate, with more pronounced effects where temperature and precipitation were extremely high or low.

Main conclusions This meta-analysis reveals the overall magnitude and direction of the effects of biological invasions on major GHG emissions, demonstrates that the effects vary substantially by GHGs, biological and environmental factors and proposes avenues for future research. These results highlight the importance of considering species traits and local and climatic conditions in assessing and managing biological invaders.

Keywords

Alien species, carbon sequestration, climate condition, ecosystem service, GHG, global change, global warming potential, invasion ecology, meta-analysis, non-native species.

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INTRODUCTION

Biological invasion by exotic species is a significant element of global environmental change that alters biodiversity and ecosystems world-wide, and ultimately the delivery of ecosystem goods and services that are critical to society (Scholes *et al.*, 2005; Ehrenfeld, 2010; Bellard *et al.*, 2014). Of particular concern are effects that alter the capacity of ecosystems to regulate or mitigate greenhouse gas (GHG) emissions – a crucial biogeochemical climate service (Anderson-Teixeira *et al.*, 2012), especially in an era of changing climate. A decline in or loss of this service may cumulatively affect climate – a core planetary boundary that has already been exceeded by human perturbations (Steffen *et al.*, 2015). While mounting literature has reported effects of biological invasions on GHG emissions, quantitative syntheses investigating the general pattern of effects across large geographic regions and identifying the sources of variation in those effects are still lacking. Such broad-scale assessment could improve our ability to generalize and predict when and where effects might be most pronounced.

The production of GHGs – primarily nitrous oxide (N₂O), methane (CH₄) and carbon dioxide (CO₂) – is related to various ecosystem processes: CO₂ is emitted through ecosystem respiration and can be offset by primary production; CH₄ is produced through methanogenesis and consumed by methanotrophy; and N₂O production is governed by microbial nitrification and denitrification processes. Previous studies have indicated that invasive species can switch ecosystems from a net source to a sink of GHGs, or vice versa, mainly through alteration of carbon and nitrogen cycles (Liao *et al.*, 2008; Ehrenfeld, 2010). Replacement of native sagebrush by exotic annual grasses in the Great Basin in the USA, for example, has resulted in a net loss of carbon over a large area (Prater *et al.*, 2006). In contrast, exotic plant invasions could also enhance an ecosystem's capacity to sequester carbon because invasive plants may have a longer growing season and higher leaf area and photosynthetic rates than natives (Baruch & Goldstein, 1999). Similarly, the net N₂O and CH₄ fluxes have also been observed to increase (e.g. *Spartina alterniflora*, Cheng *et al.*, 2007; *Morella faya*, Hall & Asner, 2007) or decrease (e.g. *Phalaris arundinacea*, Kao-Kniffin *et al.*, 2010; *Trapa natans*, Tall *et al.*, 2011) following invasions. Overall, studies addressing the effects of biological invasions on GHG emissions have shown mixed, even contradictory results, and the general pattern across species over large spatial scales remains obscure.

Previous syntheses have revealed effects of invasive alien species on ecosystem carbon and nitrogen cycling (Ehrenfeld, 2003; Liao *et al.*, 2008; Vila *et al.*, 2011). However, most of these studies have focused on alien plants, and few have examined effects from a range of taxonomic groups (Pysek *et al.*, 2010). Invasions by animals such as insects and invertebrates are equally widespread, and have been demonstrated to exert important and sometimes cascading effects on ecosystem processes and functioning (Schmitz *et al.*, 2014). In addition, few studies have explicitly linked the effects of invasions to GHG-regulating or -mitigating services that underpin human

wellbeing. Moreover, the literature has revealed substantial heterogeneity of effects across studies. A recent review also highlighted this heterogeneity, and the importance of not only quantifying the magnitude but also identifying the sources of variation in effects (Hulme *et al.*, 2013). An array of biological or environmental factors such as functional traits, recipient ecosystems, soil or climate have been suggested to contribute to variability in effects (Pysek *et al.*, 2012; Castro-Diez *et al.*, 2014). Nevertheless, how these factors could mediate the effects of invasions on GHG fluxes has not been tested at a global scale.

In this study, a structured meta-analysis of published studies was performed to synthesize the effects of biological invasions on GHG emissions and identify the factors that explain the variation in effects. Three major GHGs – N₂O, CH₄ and CO₂ – were considered. For N₂O and CH₄, I included studies that compared net changes in N₂O and CH₄ fluxes as a consequence of invasions after an explicitly reported experimental period. However, for CO₂, few studies reported effects on net carbon exchange or whole-ecosystem carbon balance. Hence, besides assessing total ecosystem carbon (TEC), I also examined the other two primary carbon pools that are especially vulnerable to invasion – soil organic carbon (SOC) and aboveground biomass carbon (AGB) – after a clearly defined experimental period. Specifically, this study addresses the following questions: (1) What is the magnitude and direction of the effects of biological invasions on GHG emissions and ecosystem carbon content? (2) Do effects differ according to the properties of invaded sites, invasive taxa and methodological aspects? (3) For exotic plant invasions, do effects vary by functional groups of N-fixation and life-form? (4) How do effects of invasions on GHG emissions vary with climate conditions? Due to constraints on the number of available studies, Question 4 was only addressed for ecosystem carbon content.

MATERIALS AND METHODS

Literature search and data extraction

A literature search of peer-reviewed publications quantifying the effects of invasive alien species on GHG emissions and carbon content was performed using the ISI Web of Science database on 20 March 2014. The search terms in Table 1 were used with no restrictions on publication year. These terms were chosen to select studies quantifying or inferring effects of invasions at the ecosystem level. The reference lists from all retrieved articles and recent syntheses (e.g. Liao *et al.*, 2008; Vila *et al.*, 2011) were also screened for other relevant publications. This resulted in an initial set of 55, 68 and 692 articles on N₂O, CH₄ and carbon content, respectively (Table 1), from which the following criteria were adopted for data inclusion.

1. Replicated studies that were either observational (i.e. examined natural invasions in the field without manipulation) or experimental (i.e. removal or addition experiments) were included.
2. Studies that explicitly mentioned the identity of invasive alien species causing effects, and quantitatively compared any of

Table 1 Keyword sequences used for the primary literature search for this meta-analysis. Peer-reviewed journal articles in the ISI Web of Science database were extracted using the search term (invader* OR invasive* OR invasion* OR exotic species OR alien species OR nonnative species) AND (ISI keyword sequences listed below) for each greenhouse gas (GHG).

GHG emissions	ISI keyword sequences	Search results	Included studies
N ₂ O emissions	(Nitrous oxide OR N ₂ O) AND (emission* OR flux* OR uptake*)	55	11
CH ₄ emissions	(Methane OR CH ₄) AND (emissions* OR flux* OR uptake*)	68	5
Ecosystem carbon content	(Carbon AND (storage OR sequestration OR loss* OR stock*)) OR ('net ecosystem exchange' OR 'net CO ₂ exchange' OR NEE)	692	52

the response variables in Table 1 between invasive species/invaded site and native species/non-invaded site, were included.

3. 'Invasive' clearly refers to alien species with self-sustained populations and the potential to spread beyond their native range. Studies addressing effects of expanding or colonizing native species such as 'woody or shrub encroachment' were excluded.

4. Studies on a single alien species rather than multispecies alien assemblages were included.

5. Studies simultaneously measuring variables in invasive species/invaded site versus native species/non-invaded site under the same environmental conditions with the intent of controlling or minimizing influences of other factors were included.

These criteria reduced the initial number of articles to 11, 5 and 32 for N₂O, CH₄ and ecosystem carbon content, respectively (see Appendix S1 in Supporting Information for full bibliographic references). The following criteria were then adopted to determine units of analysis.

1. When the same article examined different invasive species, ecosystem types or more than one response, each of them was considered as an independent case because they represented different examples of ecological effects, matching the criteria of other meta-analyses (e.g. Vila *et al.*, 2011; Castro-Diez *et al.*, 2014).

2. When the studies reported more than one value for the same pair (sampling at different locations or times), I pooled effect sizes and variances across all reported values by doing a separate meta-analysis, and used estimated pooled mean effect size and mean variance in final analysis to avoid pseudo-replication (Borenstein *et al.*, 2009).

3. If several native controls were available for the invasive species, either of the following criteria was adopted: select the most abundant and most similar to the invasive if applicable, otherwise pool the effects across all potential invasive-native control pairs.

4. Where the studies examined effects of different degrees of invasion (e.g. heavily versus less invaded sites) and different residence times (e.g. recent versus old invasions), only the putative largest contrasts were considered (Vila *et al.*, 2011).

5. If the studies involved manipulation of other ecological factors such as water availability, CO₂ level or light conditions, only non-manipulated cases were considered.

For each case study, I extracted mean, standard error (SE) or standard deviation (SD) ($SE = SD/\sqrt{n}$), and sample size (N) for both invasive species/invaded site and native species/non-invaded site for each response variable, either from tables or graphs using the DATATHIEF II software (<http://www.datathief.org>). I also recorded information on recipient ecosystem, geographic location, invasive taxa, study type and duration for each case (Table 2). In addition, invasive alien plants were further grouped into N-fixers (including both symbiotic and associative fixers, e.g. *Myrica*, *Acacia* and *Spartina*) and non-N-fixers, and into woody and herbaceous plants. Herbaceous plants were further split into graminoids and forbs. Moreover, climate variables were obtained from the WorldClim database (<http://www.worldclim.org>, Hijmans *et al.*, 2009) based on coordinates or site names reported in the article. WorldClim provides 50-year (1950–2000) average temperature and precipitation data, allowing one to test for how the effects of invasions vary along climatic gradients.

Statistical analysis

Hedge's d was calculated to estimate the effect size for each case study. This index weights cases by their number of replicates and the inverse of their variance, and is not biased by small sample sizes and unequal variances (Koricheva *et al.*, 2013). Hedge's d is a unit-free index and ranges from $-\infty$ to $+\infty$. Large effect sizes come from cases with a large difference in response between invaded and non-invaded sites (or invasive and native species) but low variability. Zero d -values indicate no difference, whereas positive and negative d -values denote a general increase and decrease trend in response variable, respectively following invasions. Hedge's d calculations and subsequent statistical analyses were conducted using METAWIN v.2.1 (Rosenberg *et al.*, 2000).

To determine the general pattern of effects (Question 1), grand weighted mean effect sizes (d^+) across all case studies were calculated for each GHG using a random-effects model, where the weight of each case is the reciprocal of its sampling variance. A random-effects model was preferred because it accounts for the fact that there is a random component of variation in effect sizes among studies besides sampling error alone (Castro-Diez *et al.*, 2014). The bias-corrected 95% bootstrap confidence interval (CI) of d^+ was calculated with 1000 iterations, to test

Categorical variables	Levels	N ₂ O emission		Ecosystem carbon content	
		<i>Q</i> _{between}	<i>P</i>	<i>Q</i> _{between}	<i>P</i>
Ecosystem	Forest	4.10	0.06	16.87	0.00
	Grassland				
	Wetland				
Study type	Experimental	0.32	0.57	0.14	0.71
	Observational				
Study duration	Short (< 1 year)	0.01	0.95	6.03	0.02
	Long (> 1 year)				
Insularity	Island	0.04	0.84	0.79	0.37
	Mainland				
Invasive taxa	Plant	2.44	0.12	19.75	0.00
	Animal				
Nitrogen fixing*	N-fixing	3.20	0.07	5.02	0.03
	Non-N-fixing				
Woodiness*	Woody	0.41	0.52	3.41	0.06
	Herbaceous				

Bold indicates significance at the $P < 0.10$ level.

*Indicates analysis only performed for exotic plant invasions.

whether d^+ differed significantly from zero (i.e. no effect of invasions) (Rosenberg *et al.*, 2000). I also tested whether effect sizes across studies were homogeneous using the Q_{total} statistic. A significant Q_{total} indicates that the variance of effect sizes among studies is greater than expected by sampling error alone, and implies some underlying structure to the data.

A structured meta-analysis was then performed to test whether heterogeneity of effects could be explained by the properties of invaded sites, invasive taxa and methodological aspects (Question 2), and whether effects varied by functional groups of N-fixation and life-form for exotic plant invasions (Question 3). To provide robust results, analyses were only performed for responses or groups with a sufficient number of studies. For categorical comparisons, the significance of between-group heterogeneity (Q_{between}), which describes whether variation in effect sizes can be attributed to differences between categories, was assessed with a chi-squared test (Rosenberg *et al.*, 2000). A random-effects model was chosen because its assumptions are more likely to be satisfied in ecological data synthesis (Rosenberg *et al.*, 2000).

To address Question 4, multivariate meta-regressions fitted with generalized least squares (GLS) were performed to test whether effect sizes varied with climate variables. A quadratic term was included in the model if visual inspection of scatterplots indicated potential nonlinearities. Meta-regressions were performed separately for plant and animal invasions because they were expected to respond in distinct ways to climate. The Akaike information criterion (AIC) was then used to rank and compare alternative models (Burnham & Anderson, 2002); the model with the lowest AIC value was selected. The Cochran Q -test (Q_c) of heterogeneity was performed to assess the significance of the model, and slope significance was also estimated. Partial residual plots were created to demonstrate

Table 2 Structured meta-analysis of the effects of biological invasions on N₂O emissions and ecosystem carbon content. For each grouping variable, Q_{between} (between-group heterogeneity) and P -values are given to determine whether variation in effect sizes can be attributed to differences between categories. Analyses were performed for responses or groups with a sufficient number of studies.

relationships between mean effect size and one climate variable after accounting for the effects of other variables. Residual and normality plots were checked for model assumptions and no violations were detected. Multivariate meta-regression modelling was conducted using the 'mvmeta' package (Gasparrini, 2014) in R statistical software (R Development Core Team, 2009), and all other meta-analyses were performed using METAWIN v.2.1 (Rosenberg *et al.*, 2000).

Non-independence of effect sizes and publication bias (i.e. selective publication of articles with significant findings over those with non-significant results), two of the most frequent and critical problems in literature synthesis (Koricheva *et al.*, 2013), were also examined using METAWIN v.2.1 (Rosenberg *et al.*, 2000) (see Appendix S2 for details).

RESULTS

This dataset covered 68 case studies, among which 11, 5 and 52 were on N₂O, CH₄ and ecosystem carbon content, respectively. The majority (78%) of invasive species included were exotic plants (versus 22% exotic animals), among which 18% were N-fixers (versus 82% non-N-fixers) and 70% were herbaceous plants (versus 30% woody plants). Among herbaceous plants, 53% were graminoids and 47% were forbs. The geographical distribution of these studies was uneven across continents, varying from 10% in Asia, to 19% in Europe and 49% in North America (Fig. 1, Appendix S3). In contrast, Africa and South America were represented by only 3% of the studies. It is noteworthy that the Hawaiian Islands and New Zealand contributed to 7% and 12% of the studies, perhaps because these islands are heavily invaded by alien species and have received much attention from ecologists. Most studies have focused on one GHG at a time, and only one publication (Cheng *et al.*,

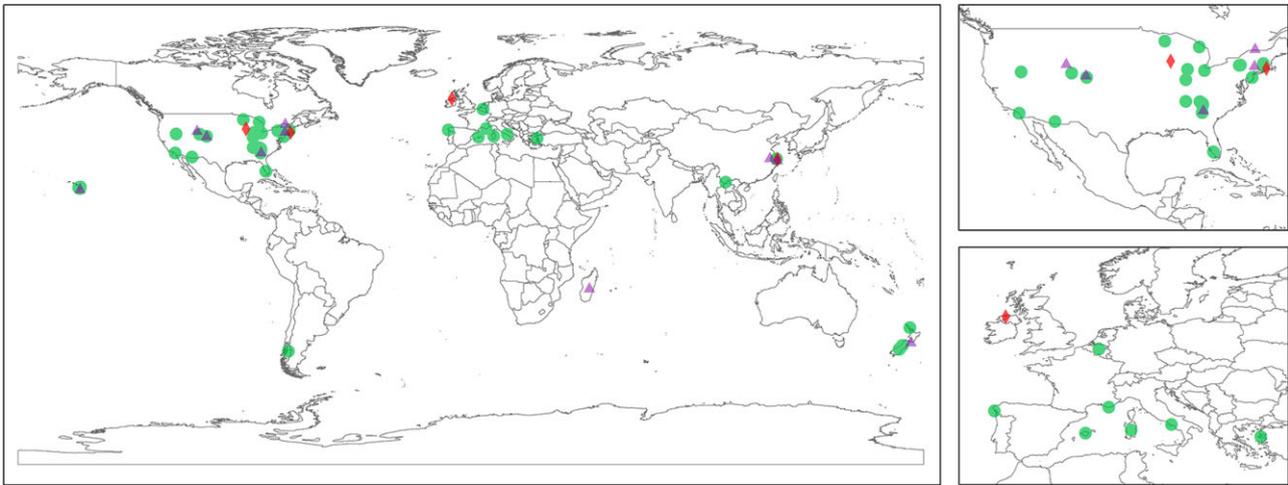


Figure 1 Global distributions of case studies included in this meta-analysis. Solid triangle, diamond, and circle symbols indicate studies on N₂O emissions, CH₄ emissions and ecosystem carbon content, respectively. Symbols are transparent and dark colours indicate an overlap of multiple studies. Insets on the right panel show details for North America and Europe.

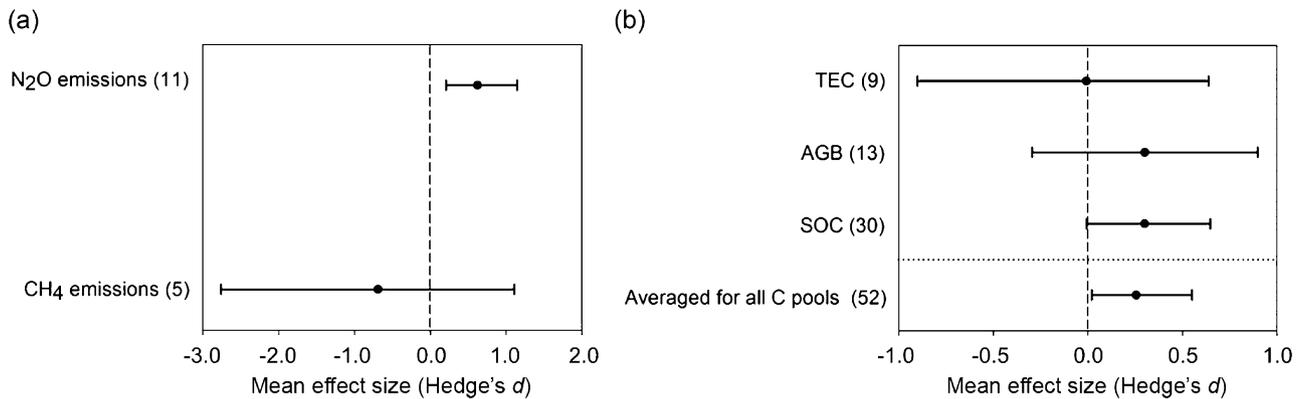


Figure 2 Mean effect sizes (Hedge's *d*) of invasions on (a) N₂O and CH₄ emissions and (b) carbon content. The latter breaks down to: total ecosystem carbon exchange or pool (TEC), aboveground biomass carbon pool (AGB), soil organic carbon pool (SOC) and averaged for all C pools. Lines indicate 95% bias-corrected bootstrap (1000 iterations) confidence intervals. In panel (a), a positive mean effect size indicates that N₂O or CH₄ emissions were increased following invasions. In panel (b), a positive mean effect size indicates that invaded sites/invasive species had on average a greater carbon stock than non-invaded sites/native species. The number of studies for each grouping of variables is given in brackets.

2007) examined simultaneous effects on two GHGs (N₂O and CH₄). All studies on CH₄ fluxes adopted experimental approaches, whereas studies on N₂O fluxes were mixed, and most studies (92%) on carbon content were based on field observations.

Effects of biological invasions on GHG emissions

The effects of biological invasions varied by each GHG of interest (Fig. 2). Overall, N₂O emissions were increased following invasions (Fig. 2a) and responses were less variable across studies ($Q_{total} = 7.01, P = 0.72$). For CH₄ emissions, the 95% CI of mean effect sizes overlapped zero (Fig. 2a), indicating that CH₄ emissions did not change uniformly with invasions. Aver-

aged across all carbon pools, there was an overall positive effect on carbon content, suggesting a general trend towards promoting carbon sequestration as a consequence of invasion (Fig. 2b). When assessed separately, different carbon pools increased by a similar magnitude following invasions ($Q_{between} = 0.79, P = 0.67$) (Fig. 2b). However, as expected, there was large heterogeneity in effects among case studies ($Q_{total} = 83.28, P = 0.005$). Comparatively, the magnitude of effect on N₂O emissions was greater than that on carbon content (Fig. 2a, b).

Determinants of the effects on GHG emissions

Among all factors considered to explain the variation in effects, ecosystem type, invasive taxa, functional traits of N-fixation and

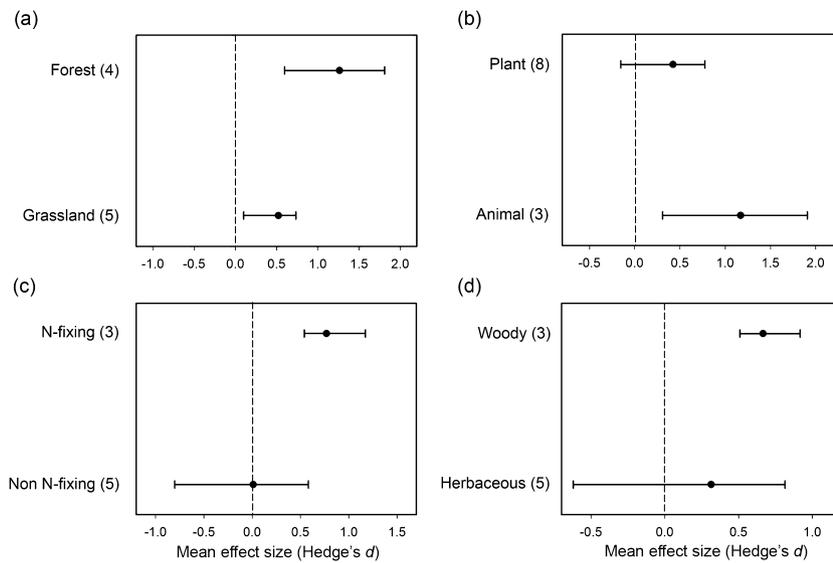


Figure 3 Mean effect sizes (Hedge's d) of invasions on N_2O emissions depending on (a) recipient ecosystem type, (b) invasive taxa, (c) functional group of N-fixation, and (d) plant life-form. Lines indicate 95% bias-corrected bootstrap confidence intervals with 1000 iterations. A positive mean effect size indicates that invaded sites/invasive species had on average greater N_2O emissions than non-invaded sites/native species. The number of studies for each grouping of variables is given in brackets.

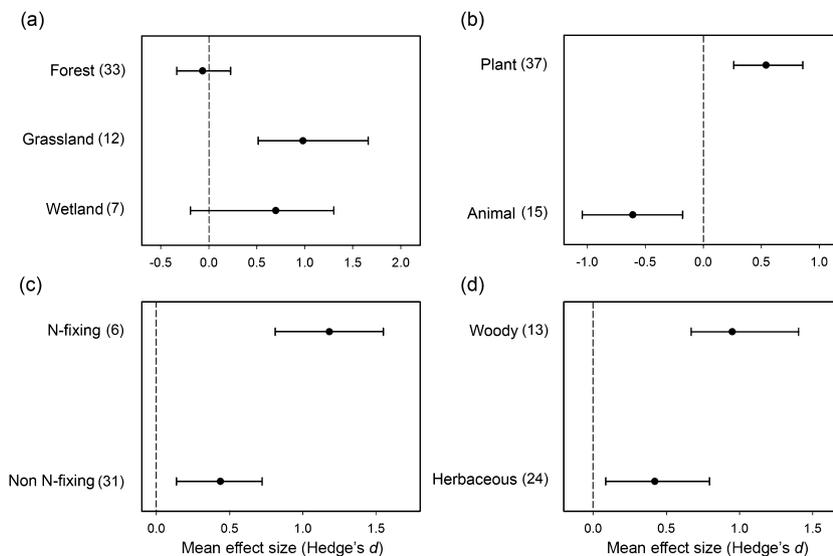


Figure 4 Mean effect sizes (Hedge's d) of invasions on ecosystem carbon content depending on (a) recipient ecosystem type, (b) invasive taxa, (c) functional group of N-fixation, and (d) plant life-form. Lines indicate 95% bias-corrected bootstrap confidence intervals with 1000 iterations. A positive mean effect size indicates that the invaded sites/invasive species had on average a greater carbon stock than non-invaded sites/native species. The number of studies for each grouping of variables is given in brackets.

life-form were the most important, whereas methodological aspects and site insularity were poor predictors (Table 2). Specifically, effects of invasions were ecosystem dependent for N_2O emissions and carbon content. N_2O emissions were increased in both invaded forest and grassland ecosystems, with a greater effect in forest (Fig. 3a). By contrast, carbon storage was enhanced in invaded grassland but did not change consistently in forest and wetland ecosystems (Fig. 4a). In addition, whether the invasive organism was an animal or plant did not affect N_2O fluxes (Fig. 3b), but mattered for effects on carbon content (Fig. 4b). Specifically, invasive alien plants tended to enhance carbon storage while animal invaders showed negative effects. Moreover, study type (observational or experimental) and site insularity (island or mainland) did not explain variation in effects across studies (Table 2). Study duration, however, did influence effects on carbon content: mean effect size differed

significantly between short-duration (i.e. less than 1 year) and long-duration (i.e. more than 1 year) studies ($d^+ = 0.40$ vs. -0.36 ; Table 2).

While focusing on exotic plant invasions, functional traits of N-fixation and life-form also explained variation in effects. Compared with non-N-fixers, the alien N-fixers had greater positive effects on N_2O emissions (though only marginally; $P = 0.07$), and on carbon content (Table 2, Figs 3c & 4c). Plant life-form did not affect N_2O fluxes, but had a marginal mediating effect on carbon content ($Q_{\text{between}} = 3.41$, $P = 0.06$): mean effect sizes were greater for invasive woody plants than for herbaceous plants (Table 2, Figs 3d & 4d). However, among herbaceous plants, effects on carbon content did not differ between invasive graminoids and forbs ($Q_{\text{between}} = 0.21$, $P = 0.67$).

Most structured meta-analyses could not be performed for CH_4 emissions due to limited data. However, qualitatively, there

Table 3 Summary statistics for comparing alternative meta-regression models for the relationship between climate variables and effect sizes (Hedge's d) of invasive plants on ecosystem carbon content: degree of freedom (d.f.), Cochran Q and significance test (P -value), and Δ AIC.

Model	d.f.	Cochran Q	P -value	Δ AIC
TEMP + TEMP ² + PPT + PPT ²	32	92.5	<0.001	0.0
TEMP + TEMP ² + PPT	33	113.6	<0.001	19.2
TEMP + TEMP ²	34	117.5	<0.001	21.1
PPT + PPT ²	34	134.9	<0.001	38.4
TEMP + PPT + PPT ²	33	133.9	<0.001	39.4
TEMP + PPT	34	149.8	<0.001	53.3

TEMP specifies 50-year (1950–2000) mean annual temperature and PPT indicates 50-year (1950–2000) mean annual precipitation. AIC, Akaike information criterion.

was a large homogeneity among the included case studies: all of them were conducted in wetland ecosystems under experimental conditions, and mostly focused on non-woody invasive plant species, such as *Phragmites australis* and *Typha angustifolia*.

Effects of invasions on GHG emissions varied with climate

Whether the effects of invasions varied with climate was tested for ecosystem carbon content. Overall, climatic factors explained variation in the effects of exotic plant invasions, and the lowest AIC meta-regression model indicated significant nonlinear relationships between effects of plant invasions on carbon content and 50-year average precipitation and temperature ($Q_C = 92.5$, $P < 0.001$) (Table 3, Appendix S4). Partial residual plots revealed stronger effects under conditions where precipitation and temperature were extremely high or low, and lesser effects where precipitation and temperature were intermediate (Fig. 5). However, no significant relationships were detected between effects of animal invasions and 50-year average climate conditions.

DISCUSSION

This study provides quantitative evidence that biological invasions have exerted significant effects on GHG emissions. Invasive alien species have increased N₂O emissions yet promoted carbon sequestration. However, the general effects on CH₄ emissions remain inconclusive. The magnitude and direction of these effects were heterogeneous and varied depending on recipient ecosystems, invasive taxa, functional traits and climatic conditions. While carbon sequestration was enhanced, the net global warming potential caused by invasions remains unresolved. It is likely that additional carbon sequestered by invaders might be offset by concurrent release of other trace gases such as N₂O and CH₄ that have greater radiative forcing (IPCC, 2007).

Effects of invasions on N₂O and CH₄ emissions

One of the most striking findings is how few studies have examined the effects of invasions on N₂O and CH₄ emissions. Ehrenfeld (2003) noted that the way in which biological invasions alter nitrification and denitrification – the primary processes contributing to N₂O production – were infrequently investigated. In recent syntheses regarding the effects of invasive species on nitrogen cycling (e.g. Liao *et al.*, 2008; Vila *et al.*, 2011; Castro-Diez *et al.*, 2014), few of the studies included nitrification and even fewer considered denitrification. Nevertheless, on the basis of existing studies, there was an overall increase in N₂O emissions subsequent to invasion, and this result was robust to variation in site insularity and methodology (Table 2). Vila *et al.* (2011) also found no significant difference in effects between island and mainland ecosystems, suggesting that greater invasion success, which is likely for islands where more alien species were found, does not necessarily translate to greater ecological effects (Parker *et al.*, 1999). Further analyses showed that plant and animal invaders did not differ in their effects on N₂O fluxes ($P = 0.12$; Fig. 3b), and several mechanisms might explain their increasing trends. Previous syntheses have revealed that invasive plants tended to have a higher N concentration and lower litter C:N ratio than native species, leading to faster decomposition and higher rates of N mineralization and nitrification (Liao *et al.*, 2008; Vila *et al.*, 2011; Castro-Diez *et al.*, 2014). These alterations in N processes could further increase soil NH₄⁺ and NO₃⁻ pools, and thus elevate denitrification and N₂O emissions. In fact, this meta-analysis did find moderate evidence that N-fixing plants (e.g. *Morella faya*; Hall & Asner, 2007) have caused greater N₂O emissions than non-N-fixing plants (Fig. 3c), indicating that N-fixation may be the main mechanism driving increases in N₂O emissions, especially in communities lacking N fixers. Similar conclusions were reached by Castro-Diez *et al.* (2014), who showed that N-fixers had greater effects on N pools and fluxes. On the other hand, animal invasions could increase N₂O emissions by altering microbial community structures and activities and the oxygen status of the environment (Ehrenfeld, 2010). Many animal invaders included in this analysis were exotic earthworms (e.g. *Lumbricus terrestris*; Speratti *et al.*, 2007); their activities could accelerate decomposition and provide anaerobic conditions, in which denitrification and N₂O production are likely to be enhanced (Lubbers *et al.*, 2013). Moreover, greater effects in invaded forest than grassland (Fig. 3a) could be attributed to combined effects of variations in species traits (e.g. biomass accumulation), litter composition, abiotic factors such as soil texture and moisture content associated with different ecosystem types.

Despite elevated N₂O emissions to the atmosphere, the simultaneous side effect of altered denitrification as a consequence of invasion may also be noteworthy. Denitrification is a form of anaerobic respiration process that converts NO₃⁻ into NO, N₂O or N₂ gases. The removal of NO₃⁻ from water due to accelerated denitrification by invaders can effectively reduce the transport of inorganic nitrogen to aquatic ecosystems where NO₃⁻ is considered as a contaminant, thus playing a vital role in enhancing

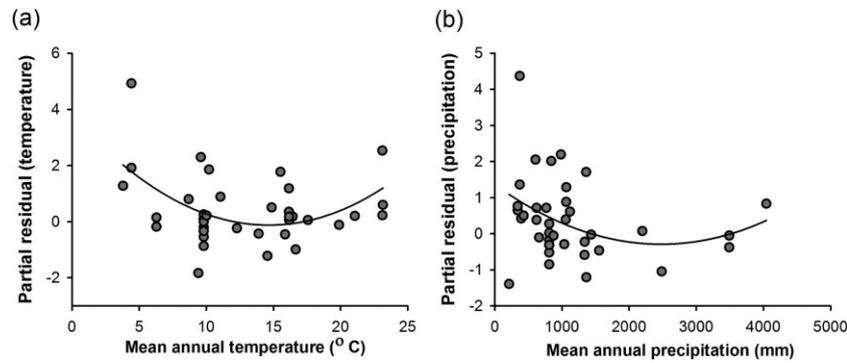


Figure 5 Variations of effects of exotic plant invasions (Hedge's d) on carbon content according to (a) 50-year (1950–2000) mean annual temperature and (b) 50-year (1950–2000) mean annual precipitation. In these partial residual plots, y values represent residuals of Hedge's d after accounting for the effects of precipitation (in panel a), or temperature (in panel b), according to the lowest Akaike information criterion meta-regression model (see Appendix S4 for model details). Partial residual plots indicated nonlinear relationships between the effects of exotic plant invasions on carbon content, and 50-year average temperature and precipitation.

water quality (e.g. the invasive macrophyte *Trapa natans*; Tall *et al.*, 2011). In particular, in wetland or riparian buffers where terrestrial and aquatic ecosystems interact this side benefit is especially important and might override the negative effect of invasions on N_2O emissions. Hence, it is critical to consider tradeoffs between N_2O emissions and NO_3^- removal both resulting from invasions of alien species. It also underscored the importance of understanding manifold consequences of invasive species and considering tradeoffs and synergies associated with these effects for improved management and conservation of multiple ecosystem services.

The general effects of invasion on CH_4 emissions were not uniform across studies. This is probably due to large variability in effects along with scarcity of available studies on CH_4 fluxes. Not surprisingly, all selected studies on CH_4 emissions were conducted in wetlands and focused on aquatic plants, because methane production from natural sources was thought to originate primarily from processes in anoxic environments. Invasive plants could enhance CH_4 emissions through increases in rhizodeposition (root exudation and rapid turnover of fine roots), stimulation of methanogenesis by providing substrates for methanogenic bacteria (Ström *et al.*, 2003) or aerenchyma that is associated with many invasive wetland plants. *Spartina alterniflora* (Cheng *et al.*, 2007) offers a good example of these mechanisms. In contrast, invasive plants could also reduce CH_4 emissions via their physical traits favouring transport of oxygen to anoxic sediments that lead to oxidation of CH_4 to CO_2 , or changes in root biomass that alter methanotroph populations (e.g. *Phalaris arundinacea*; Kao-Kniffin *et al.*, 2010). Both of these mechanisms stimulate methane consumption and reduce net emissions. However, due to limited studies, the overall effects of invasions on CH_4 fluxes need to be interpreted with caution. The generality and robustness of effects will be improved as more studies become available.

Effects of invasions on carbon content

In contrast to N_2O emissions, alien species increased carbon pools in invaded ecosystems relative to native ecosystems

(Fig. 2b). This result was robust to differences in site insularity (Table 2), again reinforcing that higher invasion success does not necessarily imply greater ecological effects. Large heterogeneity in effects on carbon content further highlighted the need for caution in predicting responses based on the mean effects (Liao *et al.*, 2008).

The structured meta-analysis further identified sources of variation in effects across studies. Invasive taxa mediated the effects of invasion, with alien plants enhancing carbon storage yet animal invaders having the opposite effect. This contrast is primarily due to difference in the mechanisms by which invaders alter ecosystems. The overall positive effect of invasive plants was in agreement with previous syntheses (Liao *et al.*, 2008; Vila *et al.*, 2011), revealing that relative to natives, invasive plants tended to increase aboveground and soil carbon pools. A similar trend has also been suggested in other narrative reviews (e.g. Raizada *et al.*, 2008; Ehrenfeld, 2010). Increases in aboveground carbon can be attributed to distinctive functional traits of invasive plants, such as a higher leaf area, higher net photosynthetic rate and longer growing season than native species (Baruch & Goldstein, 1999; Ordóñez & Olff, 2012). In addition, indirect changes in nitrogen cycling by exotic plants could also contribute to greater carbon accumulation in plant biomass (Ehrenfeld, 2003; Windham & Ehrenfeld, 2003; Allison & Vitousek, 2004). Increases in soil carbon are probably due to higher litter input and differences in litter quality and decomposition rate of invasive plants compared with native species (Liao *et al.*, 2008). Consistent with these mechanisms, this meta-analysis did find greater positive effects on carbon pools for invasive woody and N-fixing plants than herbaceous and non N-fixing plants (Fig. 4c, d). However, among herbaceous plants, effects were comparable between graminoids and forbs despite their functional differences, suggesting that linkage between traits and ecosystem-level effects is sometimes not straightforward and can be context dependent (Scharfy *et al.*, 2011; Drenovsky *et al.*, 2012). In contrary, non-native animal invaders affect ecosystem carbon content via different pathways, such as direct litter consumption (e.g. exotic earthworms), insect herbivory (e.g. hemlock woolly adelgid;

Kizlinski *et al.*, 2002), bioturbation (e.g. invasive ants), predation (e.g. *Rattus*; Wardle *et al.*, 2007) and alteration in litter, microbes and detritivores (Ehrenfeld, 2010; Peltzer *et al.*, 2010), most of which contribute to declining carbon pools. Moreover, this analysis also revealed consistent positive effects on carbon content in invaded grassland, and varied effects in forest and wetland ecosystems (Fig. 4a). Such differences might be a combined consequence of variation in the traits of invaders and mechanisms through which invaders alter ecosystems, along with environmental conditions associated with each ecosystem type.

Climate could also mediate the effects of exotic plant invasions on ecosystem carbon content. Mean effect sizes of plant invasions responded nonlinearly to 50-year mean annual temperature and precipitation (Fig. 5, Appendix S4). Stronger enhancement in carbon accumulation under warm and/or moist conditions might be explained by the fact that physiological processes and enzymatic reactions are generally faster at higher temperatures for invasive than native species, particularly if there are no other limitations such as water availability (Huxman *et al.*, 2004; Castro-Diez *et al.*, 2014). In addition, broad environmental tolerance of invasive species might also contribute to greater effects under extreme climatic conditions (Bradley *et al.*, 2010). On the other hand, under dry and/or cold conditions (which are often nutrient-poor areas), particular traits of alien plants such as N-fixation or C₄ carbon fixation could enable invaders to outperform native species and thus lead to enhanced carbon sequestration. Under conditions of intermediate temperature and precipitation the effect of invasive plants on carbon pools might be comparable to that of native species. This result provides new insights into understanding how effects of invasive species might vary across different climate gradients. With the projected warming trend and more varied precipitation, a shift in the effects of exotic plant invasions on ecosystem carbon content will be expected. The lack of relationships between effect sizes of animal invasions and climate variables, nevertheless, may suggest a possible lag or indirect responses of exotic animal invasions to climate change (i.e. mediated by plant responses) (Dukes & Mooney, 1999).

Future research needs

An important application of meta-analysis is to identify knowledge gaps (Koricheva & Gurevitch, 2014). Several future research needs can be identified from this study. First, major new efforts will be required to quantify how invasive alien species may alter emissions of N₂O and CH₄, gases that have much greater radiative forcing than CO₂. In particular, research on CH₄ emissions should not be limited to wetland or anoxic environments. A recent study (Keppler *et al.*, 2006) reported that terrestrial plants could produce CH₄ under aerobic condition, a fact which has long been neglected in empirical studies. Although the potential mechanisms still remain controversial and unclear (Nisbet *et al.*, 2009), it at least suggested another possible source of CH₄ that warrants future attention. Second,

more research focusing on the whole-ecosystem carbon balance is needed. Studies examining one or a few carbon pools might miss components such as respiration or leaching that could offset accumulated carbon, and thus lead to incomplete knowledge on the net effects of invasions. Hence, studies reporting net ecosystem exchange are favoured in order to better understand the consequences of invasions for CO₂ emissions or carbon sequestration. Third, a distinction between the long-term and short-term effects of biological invasions needs to be made. This meta-analysis showed that study duration had a significant mediating effect on carbon content (Table 2), indicating that short-term effects might not necessarily translate into long-term effects. For example, invasion of non-native earthworms in northern temperate forests increased soil carbon loss at the start of the invasion; however, in the long term, earthworm activities may contribute to carbon stabilization and therefore facilitate carbon sequestration (Zhang *et al.*, 2013). Fourth, for invaders with effects on multiple GHGs, studies are especially encouraged to address them simultaneously and convert GHG emissions to radiative forcing equivalents so that an overall net effect on global warming potential can be determined. Finally, this search of literature suggests that more research on how animal invaders affect GHG emissions is needed, particularly for N₂O and CH₄ emissions. Animals can mediate GHG release through multiple pathways, including direct consumption, stimulation of microbial activities, altering disturbance regimes, trophic interactions and so forth (Ehrenfeld, 2010). Sometimes these mechanisms can lead to multiplier or cascading effects whose magnitude may rival those currently estimated and used in literature (Schmitz *et al.*, 2014).

Methodological considerations

The primary focus of this study is the effects on GHGs directly caused by invasive alien species. Nevertheless, invasions can also indirectly affect GHGs by engaging human activities to control the spread and impacts of invasive species, which has remained largely unrecognized. One recent example revealed that GHG emissions associated with application of pesticides to control invasive *Aphis glycines* in US agricultural systems can be substantial (Heimpel *et al.*, 2013). Such indirect ways of altering GHGs through human management of invasive species are critical and deserve future attention. Moreover, studies on invasive marine species were underrepresented in this study, mostly because of methodological differences that preclude them from being analysed together with other studies in the standard meta-analysis. Qualitatively, mounting evidence suggests that invasive calcareous species (e.g. *Potamocorbula amurensis*, Chauvaud *et al.*, 2003; *Arcuatula senhousia*, Mistri & Munari, 2013) can play a prominent role in carbon cycling, and could increase the production of CO₂ in marine systems via enhanced respiration and biogenic calcification processes. Exclusion of these marine studies might lead to potential underestimates of the general effects of animal invaders on CO₂ emissions.

CONCLUSIONS

Using a meta-analytical approach, this study quantitatively summarized the effects of biological invasions on the capacity of ecosystems to regulate or mitigate major GHG emissions – a crucial ecosystem service in a changing climate. It revealed that effects were heterogeneous and varied by biological and environmental factors, and further identified knowledge gaps and proposed avenues for future research. Understanding the effects of biological invasions on GHG emissions, especially the feedback of these effects to climate systems that may produce cascading consequences, is particularly urgent in the face of rapid global environmental changes. Knowledge gained in this study could contribute to improved assessment of biological invaders. Using an ecosystem service framework for managing invasive alien species and their effects has the potential to engage a more diverse audience and could be better integrated into decision-making.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Appendix S1 Bibliographic references for studies from which data were used for this analysis.

Appendix S2 Non-independence of effect sizes and publication bias test for this meta-analysis.

Appendix S3 Proportion of case studies in different geographic regions.

Appendix S4 Parameter estimates of the lowest Akaike information criterion model for effects of exotic plant invasions on carbon content as a function of climate variables.

BIOSKETCH

Jiangxiao Qiu studies how global change drivers, including climate and land-use change, and biological invasions, affect the sustainability of freshwater and terrestrial ecosystem services using a combination of spatial simulation modelling, field experiments and landscape analysis.

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