

REVIEW AND SYNTHESIS

Invasive plants have different effects on trophic structure of green and brown food webs in terrestrial ecosystems: a meta-analysis

Matthew A. McCary,^{1*} Robin Mores,¹ Monica A. Farfan,¹ and David H. Wise^{1,2}

¹*Department of Biological Sciences University of Illinois Chicago, IL 60607, USA*

²*Institute for Environmental Science and Policy University of Illinois Chicago, IL 60612, USA*

*Correspondence: E-mail: matt.mccary@gmail.com

Abstract

Although invasive plants are a major source of terrestrial ecosystem degradation worldwide, it remains unclear which trophic levels above the base of the food web are most vulnerable to plant invasions. We performed a meta-analysis of 38 independent studies from 32 papers to examine how invasive plants alter major groupings of primary and secondary consumers in three globally distributed ecosystems: wetlands, woodlands and grasslands. Within each ecosystem we examined if green (grazing) food webs are more sensitive to plant invasions compared to brown (detrital) food webs. Invasive plants have strong negative effects on primary consumers (detritivores, bacterivores, fungivores, and/or herbivores) in woodlands and wetlands, which become less abundant in both green and brown food webs in woodlands and green webs in wetlands. Plant invasions increased abundances of secondary consumers (predators and/or parasitoids) only in woodland brown food webs and green webs in wetlands. Effects of invasive plants on grazing and detrital food webs clearly differed between ecosystems. Overall, invasive plants had the most pronounced effects on the trophic structure of wetlands and woodlands, but caused no detectable changes to grassland trophic structure.

Keywords

Biodiversity, community structure, ecosystem function, exotic species, food web, invasion biology, invasive plants, literature review, meta-analysis, trophic level.

Ecology Letters (2016) **19**: 328–335

INTRODUCTION

With the rapid rate of ecosystem degradation worldwide, it has become increasingly important to understand how humans alter ecosystem function and species diversity (Tylianakis *et al.* 2008; Powell *et al.* 2011). One main driver of anthropogenic change is the introduction of invasive alien plants into native ecosystems. Plant invasions are known to disrupt nutrient cycling and availability (Ehrenfeld 2003; Weidenhamer & Callaway 2010), alter disturbance regimes (Mack & D'Antonio 1998; Brooks *et al.* 2004) and displace native plant communities (Callaway & Aschehoug 2000; Brown *et al.* 2002). As a result, invasive plants are recognised as a major threat to natural communities across the globe (MacDougall & Turkington 2005; Moser *et al.* 2009).

Despite the documented evidence showing the negative effects of invasive plants on ecosystem functioning and dynamics, no current global-scale synthesis examines how invasive plants alter the trophic structure of ecological communities (Vila *et al.* 2011). This lack of knowledge limits generalisations about impacts of invasive plants on recipient communities and weakens our ability to predict which ecosystems are most affected by invasion. We addressed this major gap in invasion and food-web ecology by using a meta-analysis (Rosenberg *et al.* 2000; Koricheva & Gurevitch 2013) to synthesise the effects of invasive plants on higher trophic

levels (primary and secondary consumers) in terrestrial food webs.

We evaluated the impacts of invasive plants on green (grazing) vs. brown (detrital) food webs across diverse ecosystem types. Green food webs are based on living plants (McNaughton 1985); thus, the basal resource is directly impacted by a plant invader. Furthermore, herbivory can strongly affect the growth of plant populations. Detrital food webs, in contrast, are donor-controlled (DeAngelis 1980; Polis & Strong 1996), meaning that detritus affects the population dynamics of consumers but consumers have no immediate effect on detrital input (Blair *et al.* 1994; Moore & de Ruiter 2012). Because detritus and microflora are closely associated and are often consumed together, for our study 'detritus' refers to detritus and microflora as the basal resource; thus, detritivores, bacterivores and fungivores are classified as primary consumers. Due to donor-control, detrital food webs are hypothesised to be more stable than grazing food webs (Odum 1969; Neutel *et al.* 1994; Moore *et al.* 2004), leading to increased resistance against perturbations elicited by invasive plants. Brown food webs also encompass a wide diversity of feeding guilds among primary consumers, creating multiple energy channels (Oksanen *et al.* 1981) which may engender higher resistance to the effects of invasive plants. We therefore hypothesised brown food webs to be more resistant than grazing webs to plant invasions.

The impact of invasive plants on green and brown foods will likely be mediated by the characteristics of the resident plant community, i.e. the type of recipient ecosystem. Hence, we investigated how the impacts of invasive plants on green and brown webs differed between three major types of terrestrial ecosystem – wetlands, woodlands and grasslands. Plant communities differ structurally and in number of species between these three globally distributed ecosystems. Evidence suggests that naturally less-diverse and structurally simpler plant communities are more susceptible to plant invaders (D'Antonio & Vitousek 1992; Chambers *et al.* 2014), and systems that are more diverse and complex, less susceptible (Tilman 1997; Knops *et al.* 1999; Naeem *et al.* 2000). The dependence of primary and secondary consumers on basal resources is also likely to differ across ecosystems. For example, highly diverse plant communities usually support many specialist herbivores, whereas less-diverse communities harbour a higher proportion of generalists (Southwood 1978; Dyer *et al.* 2007; Pellissier *et al.* 2012). Despite these established differences, no comprehensive synthesis has been provided for how higher trophic levels of green and brown food webs respond to plant invasions in different types of ecosystems.

METHODS

Study selection

We conducted a literature search in ISI Web of Knowledge on 1 September 2015, without any restriction on year of publication, using the following string of search terms: (alien plant OR invasive plant OR exotic plant OR plant invasion OR plant invader) AND (effect OR impact) AND (food web OR food chain OR trophic OR arthropod OR invertebrate OR mammal OR bird OR amphibian OR reptile OR predator OR herbivore OR detritivore OR bacterivore OR fungivore). The initial literature search resulted in 2366 published articles. Each article was then assessed using title names and abstracts of relevant titles to determine its potential for meeting our selection criteria (detailed below) for inclusion in the meta-analysis. Following our search we then filtered the reference lists of the retrieved articles to uncover other relevant articles. During our literature review, we documented the number of articles identified and the number of studies included/excluded based on our inclusion criteria following the Preferred Reporting Items for Systematic Reviews and Meta-analysis (PRISMA; Moher *et al.* 2009) (see Appendix S1 in Supporting Information for full details).

Our main selection criterion required that peer-reviewed studies quantitatively compared the responses of food-web trophic levels in both uninvaded (i.e. 'control') and invaded (i.e. 'treatment') plots in natural or semi-natural ecosystems. Since most studies investigating the effects of invasive plants on food-web structure reported changes in abundance rather than changes in specific feeding interactions, this meta-analysis presents results in terms of positive or negative changes in abundance (i.e. showing increases or decreases in response to invasion). The term 'abundance' denotes total individuals collected per unit or trap (34 studies), biomass (2 studies), or

percentage of individuals surviving to the end of the study (2 studies) (see Appendix S2 for complete information on each study). Because only a few studies examined simultaneous changes to the basal resource, we solely analysed responses of primary and secondary consumers (Fig. 1). A study had to report changes for one or more taxonomic/functional groupings on each of these two trophic levels to be eligible for our meta-analysis. Furthermore, studies had to specifically mention how the authors characterised each grouping (e.g. springtails as fungivores, grasshoppers as herbivores, spiders as predators, etc.). To make analyses comparable between green and brown food webs, detritivores, bacterivores, fungivores and herbivores were all characterised as primary consumers; and predators and parasitoids as secondary consumers (Fig. 1). Appendix S3 has complete information on our exclusion criteria.

Meta-analysis

We collected data only from studies that reported the effects on uninvaded vs. invaded habitats with respect to plant invasion. Mean values of abundances were extracted, as well as sample size(s) and some measure of variance (i.e. standard deviation or standard error). We extracted these statistics by digitising graphs using the image processing software ImageJ (Abràmoff *et al.* 2004) for articles that did not report means and variation of means in tables. For studies that did not

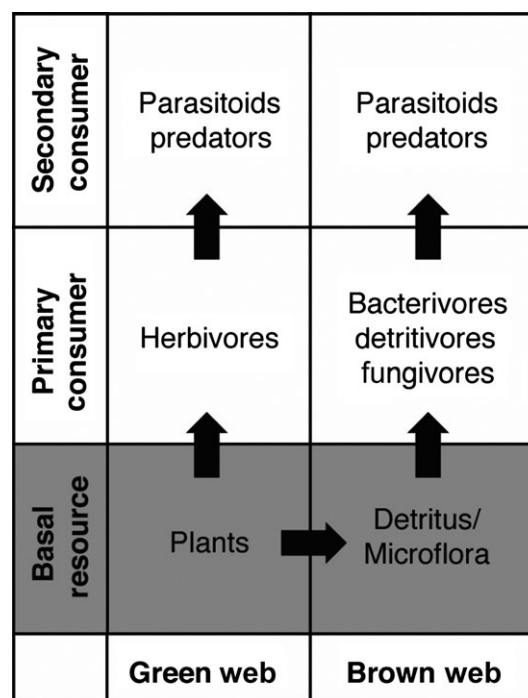


Figure 1 Our depiction of trophic structure in green and brown food webs. Because of different basal resources, the two food webs host different primary consumers but potentially similar types of secondary consumers. This meta-analysis examines the indirect effects of plant invasions on broadly defined taxonomic/functional groupings on the second and third trophic levels (i.e. the light-shaded boxes) caused by changes to the basal resources of each respective food web.

provide any form of variation ($n = 3$), we employed linear regression models on studies with complete information to provide an estimate of variance (Lajeunesse 2013). This form of within-study imputation is a reliable, yet simple, approach for estimating missing values in a given data set (Buck 1960; Pigott 1994). After retrieving all relevant information, we calculated effect sizes as *Hedges' d* (Hedges & Olkin 1985), which was chosen because it corrects for differences in sampling effort among studies and adjusts for small sample size (Rosenberg *et al.* 2013). Negative values of *Hedges' d* denote lower abundances of organisms in invaded plots compared to control plots, and vice versa. For each food web/ecosystem combination ($n = 6$), we used a mixed-effect model using the restricted maximum likelihood estimator (REML) to calculate (1) $P(Q_M)$ as a measure of the probability that effect size, d , differed between trophic levels; (2) $(1 - I^2)$ as a measure of the proportion of variance in d explained by differences between trophic levels; and (3) for each trophic level, the 95% CI for d (full details of our analysis is in Appendix S4). We also estimated the influence of publication bias (Duval & Tweedie 2000). We found no evidence of bias in any of our analyses (Appendix S4).

If a publication reported results for more than one ecosystem with at least two replicates for both control and treatment in each location, we regarded each as an independent study. When a study yielded data on multiple taxa within feeding categories (i.e. fungivore, herbivore, predator, parasitoid, etc.), only the taxonomic/functional group with the highest abundance was used to avoid pseudoreplication. If data for multiple years were given, we used the final year. All data analyses were performed with R 3.1.2 using the 'metafor' package (R Development Core Team 2014).

RESULTS

Overview of data set

The 38 independent studies from 32 research articles yielded 98 observations of responses to invasive plants [after removing three outliers (more than ± 3 SD of the mean); excluding these points did not influence the pattern of results; refer to Appendix S4]. Most articles reported on research conducted in North America (50%), followed by Europe (34%) and New Zealand (6%). Four out of five articles reported results for herbaceous invasive plants. Most articles focused on brown (38%) or green (33%) food webs, with the remaining articles (29%) reporting various aspects of green and brown webs in the same location [although only three of the 32 articles (10%) comprehensively studied each trophic level for both green and brown food webs]. The three ecosystem types were represented in similar proportions (30–40%). See Appendix S5 for the complete list of studies used in the meta-analysis.

Wetlands

In wetland ecosystems invasive plants altered abundances of both primary and secondary consumers in green food webs, but in opposite directions (Fig. 2a; $P(Q_M) = 0.027$, $1 - I^2 = 35\%$, d.f. = 1). Primary consumers responded

negatively to plant invasions (mean $d = -0.65$, CI = $-0.97/-0.34$), secondary consumers positively (mean $d = 0.56$, CI = $0.06/1.1$).

In contrast, plant invaders had no discernable impact on brown food webs in wetlands (Fig. 2a; $P(Q_M) = 0.21$, $1 - I^2 = 12\%$, d.f. = 1). Neither primary (CI = $-0.14/0.79$) nor secondary consumers (CI = $-1.2/0.27$) responded consistently to plant invasions.

Woodlands

In woodlands plant invaders affected the green food web but only on one trophic level (Fig. 2b; $P(Q_M) = 0.35$, $1 - I^2 = 33\%$, d.f. = 1). As in wetlands, primary consumers were less abundant in invaded plots (mean $d = -0.57$, CI = $-1.1/-0.02$) (Fig. 2b), but densities of secondary consumers did not substantially differ between control and invaded conditions (CI = $-1.2/0.63$).

Unlike the pattern for wetlands, brown food webs in woodlands appear to have been affected by invasive plants, and differently across trophic levels (Fig. 2b; $P(Q_M) = 0.08$, $1 - I^2 = 11\%$, d.f. = 1). Primary consumers responded negatively to plant invasions (mean $d = -0.57$, CI = $-1.2/0.04$), whereas secondary consumers responded positively (mean $d = 0.91$, CI = $-0.11/1.92$). The pattern of effects across trophic levels for the green food web in wetlands is similar to the pattern for brown food webs in woodlands [Fig. 2a (green) vs. Fig. 2b (brown)], but statistical support for the woodland pattern is weaker.

Grasslands

In sharp contrast to wetlands and woodlands, invasive plants had no detectable impact on either primary or secondary consumers in grasslands [Fig. 2c; $P(Q_M) = 0.39$, $1 - I^2 = 2\%$ (green web); $P(Q_M) = 0.93$, $1 - I^2 = 12\%$ (brown web)].

DISCUSSION

Invasive plants can alter abundances of major taxa of primary and secondary consumers in terrestrial food webs, but the pattern is complex. The direction and magnitude of these effects vary across trophic levels of green and brown food webs and the type of recipient ecosystem (Fig. 3). Invasive plants had no detectable impact on higher trophic levels in grasslands, had strong effects, but in opposite directions, on upper trophic levels of green food webs in wetlands; and altered abundances on at least one trophic level of both green and brown webs in woodlands. Understanding possible mechanisms underlying these broad differences in the impacts of plant invasions on higher trophic levels will aid in predicting future changes to native communities.

Impacts of invasive plants on green food webs

We hypothesised that upper trophic levels of brown food webs would be impacted less than those of green webs. The pattern for wetlands and woodlands supports this conjecture (Fig. 3a,b); invasive plants tended to have stronger, clearer

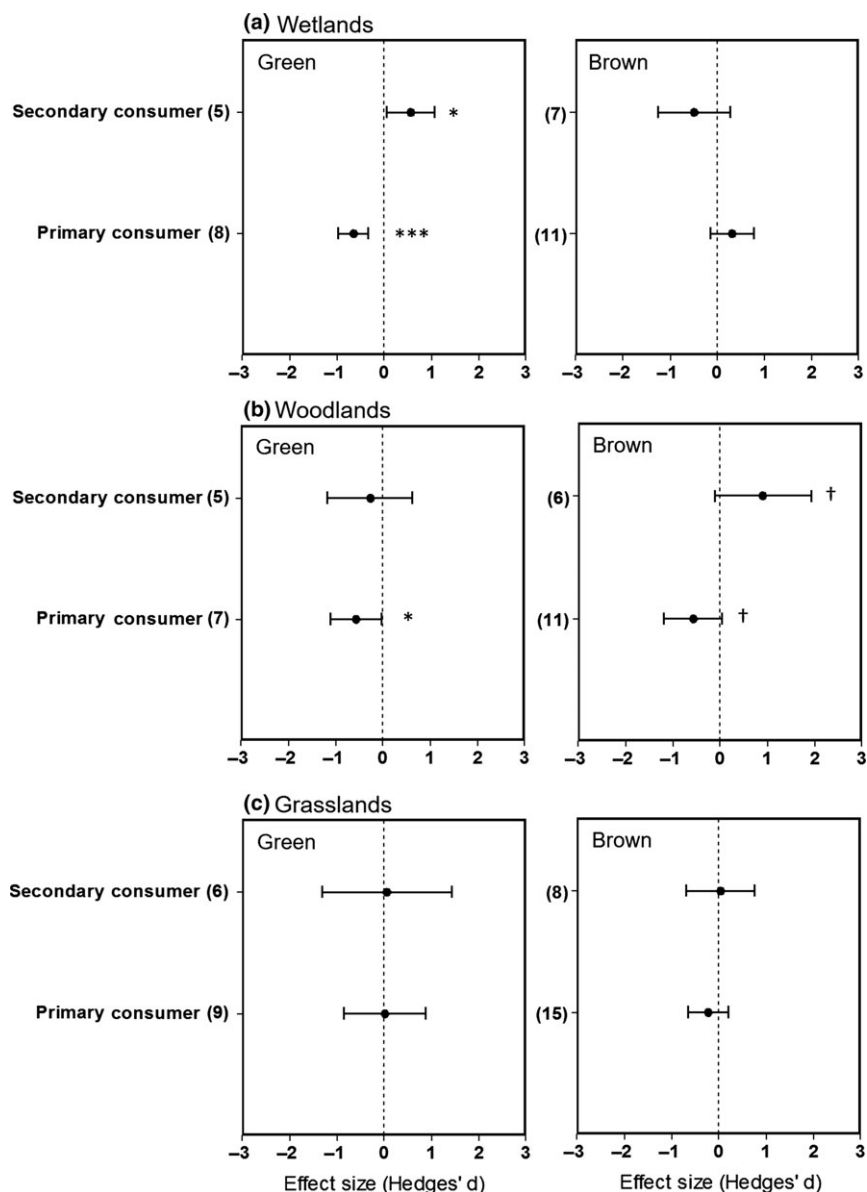


Figure 2 Mean effect size (*Hedges' d*) of invasive plants on food webs in (a) wetland, (b) woodland and (c) grassland ecosystems. Positive effect sizes indicate that the invaded plots had greater abundance than non-invaded (control) plots. Means of *d* are shown with 95% CI; number of taxonomic/functional groups analysed for each trophic level appears in parentheses. (***) indicates $P < 0.001$ for null hypothesis that effect size = 0; (*) denotes $P < 0.05$; (†) denotes $P < 0.10$.

impacts in the green food webs. The pattern in grasslands is not supportive because no effects were observed in either green or brown food webs (Fig. 3c). These patterns do support the hypothesis that green food webs are more vulnerable to invasive plants in less-diverse ecosystems, i.e. wetlands compared with grasslands. Multiple trophic levels in grassland food webs may exhibit large amounts of functional redundancy (Tilman & Downing 1996; Diaz & Cabido 2001; Zavaleta *et al.* 2010). Thus, even though an invasive plant may eliminate or lower densities of several native plant species, high functional redundancy reduces the probability that removing one or several links will lead to system instability (Memmott *et al.* 2006; Solé & Montoya 2006). Our meta-analysis included some very-diverse

grassland ecosystems (e.g. Belnap & Phillips 2001; Belnap *et al.* 2005; and Lescano & Farji-Brener 2011), the likely reason it revealed no consistent impact of invasive plants on the grazing food web. In addition, the high species richness of grasslands may mean that the system is less likely to become dominated by a single invasive plant (Tilman 1997; Kennedy *et al.* 2002). A novel invader might not substantially reduce foraging options for herbivores (and consequently, their predators). Mobile herbivores will still be able to track their preferred resource while ignoring the presence of the plant invader (Berg *et al.* 2010), resulting in minimal changes to primary and secondary consumers in response to plant invasions.

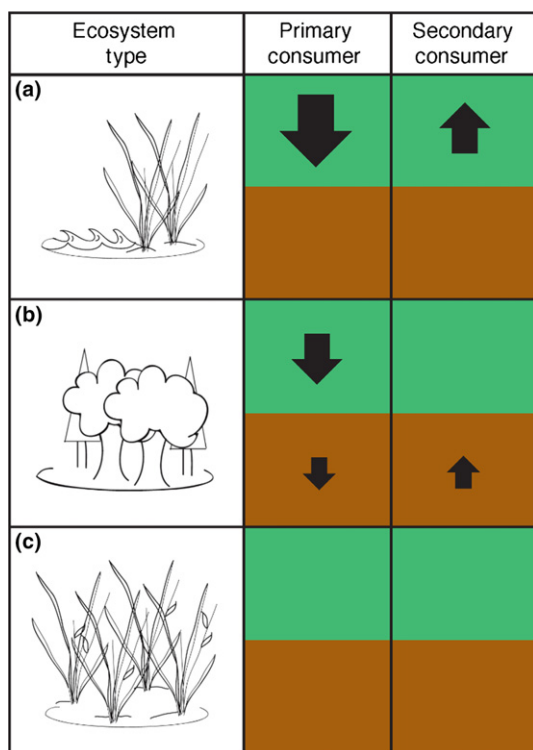


Figure 3 Conceptual diagram illustrating the summarised effects of invasive plants on trophic structure of green and brown food webs in (a) wetlands, (b) woodlands and (c) grasslands. The direction of the arrow indicates either a positive (upwards) or negative (downwards) effect on the abundance of primary and secondary consumers. Open boxes illustrate no effect. Large arrows denote $P < 0.001$; intermediate arrows indicate $P < 0.05$; small arrows denote $P < 0.10$.

In contrast to grasslands, wetlands exhibited considerable shifts in the structure of their green food webs. Wetland ecosystems are highly susceptible to invasive plants and are more prone to result in monocultures following invasion (Zedler & Kercher 2004; Ström *et al.* 2014). A drastic shift in the dominance of one plant will limit resource options for a variety of herbivores, leading to a decline in abundance. Furthermore, net primary productivity (NPP) has been documented to increase following a plant invasion in wetlands (Ehrenfeld 2003; Angeloni *et al.* 2006; Liao *et al.* 2007). Taller and denser vegetation will create more resident opportunities for a number of arthropod predators, such as web-building spiders (Finke & Denno 2002; Langellotto & Denno 2004). The combination of less-available resources coupled with increases in predator load in the aboveground vegetation will lead to reductions in herbivore populations due to both bottom-up and top-down forces. For instance Engelkes *et al.* (2012) discovered that invasion of a riparian zone by *Rorippa austriaca* and *Senecio inaequidens* led to significantly reduced herbivore abundance compared to native plant communities. They found that herbivores demonstrated less success on non-native plants (bottom-up control) and were subject to higher rates of predation pressure (top-down control). Such interactions between changing vegetation structure and population control processes could lead to negative responses to invasions by primary consumers while secondary consumers

become more abundant (e.g. Harvey *et al.* 2010; Engelkes *et al.* 2012).

Primary consumers of woodland green food webs also tended to decline in response to invasive plants. Similar to wetlands, woodland understories are highly vulnerable to plant invasions (Knight *et al.* 2007; Asner *et al.* 2008), with consequent effects on primary consumers. Simao *et al.* (2010) evaluated impacts of forest invasion by *Microstegium vimineum* on arthropod food webs. Plots with *M. vimineum* had reduced native-plant richness and lowered numbers of herbivores and their predators. Food-web theory predicts that a scarcity of food options will cause declines in abundances of higher trophic levels (Pimm *et al.* 1991; Osenberg & Mittelbach 1996). This likely occurred in several woodland green food webs in our meta-analysis, but many clearly showed the opposite pattern, judging from the broad overlap in the confidence intervals for secondary consumers in the green web (Fig. 2b). Predators in these studies may have been feeding in both green and brown food webs, i.e. multi-channel omnivory (e.g. Polis & Strong 1996). Even when vegetation complexity is greatly reduced by plant invasion, predators in green food webs may shift from a plant-based to a detritus-based food chain (Miyashita *et al.* 2003; Shimazaki & Miyashita 2005; Haraguchi *et al.* 2013). While not all predators in woodland habitats are capable of switching food channels in response to plant invasions, such switching by many may explain the absence of responses to plant invasion by secondary consumers in this type of ecosystem.

Invasive plants impact on brown food webs

This meta-analysis found no evidence that primary and secondary consumers in brown food webs of wetland and grassland ecosystems responded to plant invasion. Because much less standing detritus is present in these ecosystems compared to woodlands (Cadisch & Giller 1997), an invasion by a novel plant may lead to negligible changes in energy flow through brown food webs. Most (82%) invaders of wetlands and grasslands in this study were herbaceous species, likely resulting in minimal changes in the amount of standing plant litter because of rapid decomposition. Although dramatic changes in the structural habitat may arise following a plant invasion (Zedler & Kercher 2004; Hejda *et al.* 2009), lack of major changes to detrital input – the fuel of brown food webs – could explain why our meta-analysis did not detect changes in the upper trophic levels of brown food webs in both wetland and grassland ecosystems.

In contrast to our expectation, brown food webs in woodland ecosystems appear to be more sensitive to plant invasions than the green web, or at least equally sensitive (given the degree of overlap of CI of d 's with zero; Fig. 2b). Several plant invaders of woodland habitats can alter standing stocks of leaf litter and other plant detritus (Ehrenfeld *et al.* 2001; Allison & Vitousek 2004). Alteration of litter quantity and quality can affect abundances of detritivores, fungivores and bacterivores – either directly through changes in toxicity and palatability, or indirectly through effects on the microflora (Topp *et al.* 2008; Wolkovich *et al.* 2009). Kappes *et al.* (2007), for example, demonstrated that invasive giant

knotweed (*Reynoutria* spp.) negatively impacted gastropods and other detritivores in a floodplain forest. The effect was due to the high input of highly acidic *Reynoutria* litter, which lowered soil pH and moisture. There are also several other invasive plants with similar impacts on primary consumers in the brown food web of woodland ecosystems (Bassett 2014; McCary *et al.* 2015; Motard *et al.* 2015). On the contrary, increased detrital inputs from invasive plants might actually favour secondary consumers on the forest floor by altering the structure of the litter layer (Bultman & Uetz 1982; Mgbodzi *et al.* 2008). Increased depth and complexity of the leaf litter could provide added cover and foraging options for ground-dwelling arthropod predators (Uetz 1979; Bultman & Uetz 1984). The majority of woodland studies in this meta-analysis featured arthropod predators such as spiders and ground beetles, which could help explain the positive responses of secondary consumers in this meta-analysis.

Future directions and conclusions

This synthesis is an initial attempt to understand how invasive plants alter higher trophic levels of terrestrial systems – an element of both food-web ecology and invasion biology that requires much more attention (Mommott *et al.* 2006; Vila *et al.* 2011). The results of this meta-analysis suggest several fruitful avenues of future research: (1) More research is needed on the vertebrate components of the second and third trophic levels, as most studies in our meta-analysis focused on the impacts of invasive plants on invertebrate-dominated food webs. (2) Future studies that investigate simultaneous changes in all three trophic levels are needed, i.e. changes to the basal resource as well as indirect effects on primary and secondary consumers. (3) Effects of invasive plants should be explored simultaneously in both green and brown food webs on the same site; only a few articles ($n = 3$) comprehensively met this criterion. Because these webs are intrinsically linked (Fig. 1), generalisations about differential impacts on green and brown webs will be much stronger if they are based upon research on the same site.

Knowing how invasive plants alter food-web structure and dynamics, including linkages between belowground and aboveground systems, is critical for forecasting future changes to recipient communities (Ings *et al.* 2009; Bardgett & Wardle 2010; Ricciardi *et al.* 2013). Our synthesis reveals that invasive plants alter the trophic structure of detritus-based and/or grazing food webs in wetlands and woodlands, but not in grasslands. We hope this synthesis promotes future research that will enable us to evaluate further the robustness of this pattern.

ACKNOWLEDGEMENTS

We thank the four anonymous reviewers for substantially improving the quality of this manuscript. Discussions with Emily Minor (University of Illinois at Chicago), Nicholas Barber (Northern Illinois University) and the Wise lab group at UIC (Nolan Bielinski, Amanda Henderson, Brook Herman, Susan Kirt and Cristian Martínez) greatly assisted in the overall conceptualisation and design of this study. Many

thanks to the authors of the original studies included in our meta-analysis.

AUTHORSHIP

MM wrote last versions of manuscript, designed study and performed the meta-analysis. RM contributed to initial versions of manuscript, designed study and conducted literature search. MF contributed to initial versions of manuscript, designed study and conducted literature search. DW provided intellectual guidance, assisted with the meta-analysis. All authors contributed substantially to revisions.

REFERENCES

- Abramoff, M.D., Magalhães, P.J. & Ram, S.J. (2004). Image processing with ImageJ. *Biophotonics international*, 11, 36–42.
- Allison, S.D. & Vitousek, P.M. (2004). Rapid nutrient cycling in leaf litter from invasive plants in Hawaii. *Oecologia*, 141, 612–619.
- Angeloni, N.L., Jankowski, K.J., Tuchman, N.C. & Kelly, J.J. (2006). Effects of an invasive cattail species (*Typha x glauca*) on sediment nitrogen and microbial community composition in a freshwater wetland. *FEMS Microbiol. Lett.*, 263, 86–92.
- Asner, G.P., Hughes, R.F., Vitousek, P.M., Knapp, D.E., Kennedy-Bowdoin, T., Boardman, J. *et al.* (2008). Invasive plants transform the three-dimensional structure of rain forests. *Proc. Natl Acad. Sci.*, 105, 4519–4523.
- Bardgett, R.D. & Wardle, D.A. (2010). *Aboveground-Belowground Linkages: Biotic Interactions, Ecosystem Processes, and Global Change*. Oxford University Press, Oxford, UK.
- Bassett, I.E. (2014). Impacts on invertebrate fungivores: a predictable consequence of ground-cover weed invasion? *Biodivers. Conserv.*, 23, 791–810.
- Belnap, J. & Phillips, S.L. (2001). Soil biota in an ungrazed grassland: response to annual grass (*Bromus tectorum*) invasion. *Ecol. Appl.*, 11, 1261–1275.
- Belnap, J., Phillips, S.L., Sherrod, S.K. & Moldenke, A. (2005). Soil biota can change after exotic plant invasion: does this affect ecosystem processes? *Ecology*, 86, 3007–3017.
- Berg, M.P., Kiers, E., Driessen, G., Van Der Heijden, M., Kooi, B.W., Kuenen, F. *et al.* (2010). Adapt or disperse: understanding species persistence in a changing world. *Glob. Chang. Biol.*, 16, 587–598.
- Blair, J.M., Parmelee, R.W. & Wyman, R.L. (1994). A comparison of the forest floor invertebrate communities of 4 forest types in the Northeast United States. *Pedobiologia*, 38, 146–160.
- Brooks, M.L., D'antonio, C.M., Richardson, D.M., Grace, J.B., Keeley, J.E., Ditomaso, J.M. *et al.* (2004). Effects of invasive alien plants on fire regimes. *Bioscience*, 54, 677–688.
- Brown, B.J., Mitchell, R.J. & Graham, S.A. (2002). Competition for pollination between an invasive species (purple loosestrife) and a native congener. *Ecology*, 83, 2328–2336.
- Buck, S.F. (1960). A method of estimation of missing values in multivariate data suitable for use with an electronic computer. *J. R. Stat. Soc.*, 22, 302–306.
- Bultman, T.L. & Uetz, G.W. (1982). Abundance and community structure of forest floor spiders following litter manipulation. *Oecologia*, 55, 34–41.
- Bultman, T.L. & Uetz, G.W. (1984). Effect of structure and nutritional quality of litter on abundances of litter-dwelling arthropods. *Am. Midl. Nat.*, 111, 165–172.
- Cadisch, G. & Giller, K.E. (1997). *Driven by Nature: Plant Litter Quality and Decomposition*. CAB International, Wallingford, UK.
- Callaway, R.M. & Aschehoug, E.T. (2000). Invasive plants versus their new and old neighbors: a mechanism for exotic invasion. *Science*, 290, 521–523.

- Chambers, J., Bradley, B., Brown, C., D'Antonio, C., Germino, M., Grace, J. *et al.* (2014). Resilience to stress and disturbance, and resistance to *Bromus tectorum* L. invasion in cold desert shrublands of western North America. *Ecosystems*, 17, 360–375.
- D'Antonio, C.M. & Vitousek, P.M. (1992). Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annu. Rev. Ecol. Syst.*, 23, 63–87.
- DeAngelis, D. (1980). Energy flow, nutrient cycling, and ecosystem resilience. *Ecology*, 61, 764–771.
- Díaz, S. & Cabido, M. (2001). Vive la différence: plant functional diversity matters to ecosystem processes. *Trends Ecol. Evol.*, 16, 646–655.
- Duval, S. & Tweedie, R. (2000). A nonparametric 'trim and fill' method of accounting for publication bias in meta-analysis. *J. Am. Stat. Assoc.*, 95, 89–98.
- Dyer, L.A., Singer, M., Lill, J., Stireman, J., Gentry, G., Marquis, R.J. *et al.* (2007). Host specificity of Lepidoptera in tropical and temperate forests. *Nature*, 448, 696–699.
- Ehrenfeld, J.G. (2003). Effects of exotic plant invasions on soil nutrient cycling processes. *Ecosystems*, 6, 503–523.
- Ehrenfeld, J.G., Kourtev, P. & Huang, W. (2001). Changes in soil functions following invasions of exotic understory plants in deciduous forests. *Ecol. Appl.*, 11, 1287–1300.
- Engelkes, T., Wouters, B., Bezemer, T.M., Harvey, J.A. & van der Putten, W.H. (2012). Contrasting patterns of herbivore and predator pressure on invasive and native plants. *Basic Appl. Ecol.*, 13, 725–734.
- Finke, D.L. & Denno, R.F. (2002). Intraguild predation diminished in complex-structured vegetation: implications for prey suppression. *Ecology*, 83, 643–652.
- Haraguchi, T.F., Uchida, M., Shibata, Y. & Tayasu, I. (2013). Contributions of detrital subsidies to aboveground spiders during secondary succession, revealed by radiocarbon and stable isotope signatures. *Oecologia*, 171, 935–944.
- Harvey, K.J., Britton, D.R. & Minchinton, T.E. (2010). Insect diversity and trophic structure differ on native and non-indigenous congeneric rushes in coastal salt marshes. *Austral Ecol.*, 35, 522–534.
- Hedges, L.V. & Olkin, I. (1985). *Statistical Method for Meta-analysis*. Academic press, Orlando, FL.
- Hejda, M., Pyšek, P. & Jarošík, V. (2009). Impact of invasive plants on the species richness, diversity and composition of invaded communities. *J. Ecol.*, 97, 393–403.
- Ings, T.C., Montoya, J.M., Bascompte, J., Bluthgen, N., Brown, L., Dormann, C.F. *et al.* (2009). Ecological networks – beyond food webs. *J. Anim. Ecol.*, 78, 253–269.
- Kappes, H., Lay, R. & Topp, W. (2007). Changes in different trophic levels of litter-dwelling macrofauna associated with giant knotweed invasion. *Ecosystems*, 10, 734–744.
- Kennedy, T.A., Naeem, S., Howe, K.M., Knops, J.M.H., Tilman, D. & Reich, P. (2002). Biodiversity as a barrier to ecological invasion. *Nature*, 417, 636–638.
- Knight, K.S., Kurylo, J.S., Endress, A.G., Stewart, J.R. & Reich, P.B. (2007). Ecology and ecosystem impacts of common buckthorn (*Rhamnus cathartica*): a review. *Biol. Invasions*, 9, 925–937.
- Knops, J.M., Tilman, D., Haddad, d.N., Naeem, S., Mitchell, C., Haarstad, J. *et al.* (1999). Effects of plant species richness on invasion dynamics, disease outbreaks, insect abundances and diversity. *Ecol. Lett.*, 2, 286–293.
- Koricheva, J. & Gurevitch, J. (2013). Place of meta-analysis among other methods of research synthesis. In: *Handbook of Meta-analysis in Ecology and Evolution* (eds Koricheva, J., Gurevitch, J. & Mengersen, K.). Princeton University Press, Princeton, NJ, pp. 3–13.
- Lajeunesse, M. (2013). Recovering missing or partial data from studies: a Survey of Conversions and Imputations for Meta-analysis. In: *Handbook of Meta-analysis in Ecology and Evolution* (eds Koricheva, J., Gurevitch, J. & Mengersen, K.). Princeton University Press, Princeton, NJ, pp. 195–206.
- Langelotto, G.A. & Denno, R.F. (2004). Responses of invertebrate natural enemies to complex-structured habitats: a meta-analytical synthesis. *Oecologia*, 139, 1–10.
- Lescano, M.N. & Farji-Brener, A.G. (2011). Exotic thistles increase native ant abundance through the maintenance of enhanced aphid populations. *Ecol. Res.*, 26, 827–834.
- Liao, C., Luo, Y., Jiang, L., Zhou, X., Wu, X., Fang, C. *et al.* (2007). Invasion of *Spartina alterniflora* enhanced ecosystem carbon and nitrogen stocks in the Yangtze Estuary, China. *Ecosystems*, 10, 1351–1361.
- MacDougall, A.S. & Turkington, R. (2005). Are invasive species the drivers or passengers of change in degraded ecosystems? *Ecology*, 86, 42–55.
- Mack, M.C. & D'Antonio, C.M. (1998). Impacts of biological invasions on disturbance regimes. *Trends Ecol. Evol.*, 13, 195–198.
- McCary, M.A., Martínez, J.-C., Umek, L., Heneghan, L. & Wise, D.H. (2015). Effects of woodland restoration and management on the community of surface-active arthropods in the metropolitan Chicago region. *Biol. Conserv.*, 190, 154–166.
- McNaughton, S. (1985). Ecology of a grazing ecosystem: the Serengeti. *Ecol. Monogr.*, 55, 259–294.
- Memmott, J., Alonso, D., Berlow, E.L., Dobson, A., Dunne, J.A., Sole, R.V. *et al.* (2006). Biodiversity loss and ecological network structure. In: *Ecological Networks: Linking Structure to Dynamics in Food Webs* (eds Pascual, M. & Dunne, J.). Oxford University Press, New York, NY, pp. 325–347.
- Mgobozi, M.P., Somers, M.J. & Dippenaar-Schoeman, A.S. (2008). Spider responses to alien plant invasion: the effect of short- and long-term *Chromolaena odorata* invasion and management. *J. Appl. Ecol.*, 45, 1189–1197.
- Miyashita, T., Takada, M. & Shimazaki, A. (2003). Experimental evidence that aboveground predators are sustained by underground detritivores. *Oikos*, 103, 31–36.
- Moher, D., Liberati, A., Tetzlaff, J., Altman, D.G. & The, P.G. (2009). Preferred reporting items for systematic reviews and meta-analyses: the PRISMA statement. *PLoS Med.*, 6, e1000097.
- Moore, J.C. & de Ruiter, P.C. (2012). *Energetic Food Webs: An Analysis of Real and Model Ecosystems*. Oxford University Press, Oxford, UK.
- Moore, J.C., Berlow, E.L., Coleman, D.C., Ruiter, P.C., Dong, Q., Hastings, A. *et al.* (2004). Detritus, trophic dynamics and biodiversity. *Ecol. Lett.*, 7, 584–600.
- Moser, W.K., Barnard, E.L., Billings, R.F., Crocker, S.J., Dix, M.E., Gray, A.N. *et al.* (2009). Impacts of nonnative invasive species on US forests and recommendations for policy and management. *J. For.*, 107, 320–327.
- Motard, E., Dusz, S., Geslin, B., Akpa-Vinceslas, M., Hignard, C., Babiari, O. *et al.* (2015). How invasion by *Ailanthus altissima* transforms soil and litter communities in a temperate forest ecosystem. *Biol. Invasions*, 17, 1817–1832.
- Naeem, S., Knops, J.M.H., Tilman, D., Howe, K.M., Kennedy, T. & Gale, S. (2000). Plant diversity increases resistance to invasion in the absence of covarying extrinsic factors. *Oikos*, 91, 97–108.
- Neutel, A.-M., Roerdink, J.B. & De Ruiter, P.C. (1994). Global stability of two-level detritus decomposer food chains. *J. Theor. Biol.*, 171, 351–353.
- Odum, E.P. (1969). The strategy of ecosystem development. *Science*, 164, 262–270.
- Oksanen, L., Fretwell, S.D., Arruda, J. & Niemela, P. (1981). Exploitation ecosystems in gradients of primary productivity. *Am. Nat.*, 118, 240–261.
- Osenberg, C.W. & Mittelbach, G.G. (1996). The relative importance of resource limitation and predator limitation in food chains. In: *Food Webs* (ed. Polis, G.A. & Winemiller, K.O.). Springer Publishing, New York, NY, pp. 134–148.
- Pellissier, L., Fiedler, K., Ndrube, C., Dubuis, A., Pradervand, J.N., Guisan, A. *et al.* (2012). Shifts in species richness, herbivore specialization, and plant resistance along elevation gradients. *Ecol. Evol.*, 2, 1818–1825.
- Piggott, T.D. (1994). Methods for handling missing data in research synthesis. In: *The Handbook of Research Synthesis* (eds Cooper, H. &

- Hedges, L.V.). Russell Sage Foundation, New York, NY, pp. 163–176.
- Pimm, S.L., Lawton, J.H. & Cohen, J.E. (1991). Food web patterns and their consequences. *Nature*, 350, 669–674.
- Polis, G.A. & Strong, D.R. (1996). Food web complexity and community dynamics. *Am. Nat.*, 147, 813–846.
- Powell, K.I., Chase, J.M. & Knight, T.M. (2011). A synthesis of plant invasion effects on biodiversity across spatial scales. *Am. J. Bot.*, 98, 539–548.
- R, Core Development Team (2013). *R: A Language and Environment*. R Foundation, Vienna, Austria.
- Ricciardi, A., Hoopes, M.F., Marchetti, M.P. & Lockwood, J.L. (2013). Progress toward understanding the ecological impacts of nonnative species. *Ecol. Monogr.*, 83, 263–282.
- Rosenberg, M.S., Adams, D.C. & Gurevitch, J. (2000). *MetaWin: Statistical Software for Meta-analysis*. Sinauer Associates Sunderland, Sunderland, MA.
- Rosenberg, M., Rothstein, H. & Gurevitch, J. (2013). Effect sizes: conventional choices and calculations. In: *Handbook of Meta-analysis in Ecology and Evolution* (eds Koricheva, J., Gurevitch, J. & Mengersen, K.). Princeton University Press, Princeton, NJ, pp. 61–71.
- Shimazaki, A. & Miyashita, T. (2005). Variable dependence on detrital and grazing food webs by generalist predators: aerial insects and web spiders. *Ecography*, 28, 485–494.
- Simao, M.C.M., Flory, S.L. & Rudgers, J.A. (2010). Experimental plant invasion reduces arthropod abundance and richness across multiple trophic levels. *Oikos*, 119, 1553–1562.
- Solé, R.V. & Montoya, J.M. (2006). Ecological network meltdown from habitat loss and fragmentation. In: *Ecological Networks: Linking Structure to Dynamics in Food Webs* (eds Pascual, M. & Dunne, J.). Oxford University Press, New York, NY, pp. 305–324.
- Southwood, T.R.E. (1978). *Ecological Methods, with Particular Reference to the Study of Insect Opopulations*. Chapman and Hall, London, UK.
- Ström, L., Jansson, R. & Nilsson, C. (2014). Invasibility of boreal wetland plant communities. *J. Veg. Sci.*, 25, 1078–1089.
- Tilman, D. (1997). Community invasibility, recruitment limitation, and grassland biodiversity. *Ecology*, 78, 81–92.
- Tilman, D. & Downing, J.A. (1996). Biodiversity and stability in grasslands. In: *Ecosystem Management* (eds Samson, F. & Knopf, F.). Springer Publishing, New York, NY, pp. 3–7.
- Topp, W., Kappes, H. & Rogers, F. (2008). Response of ground-dwelling beetle (Coleoptera) assemblages to giant knotweed (*Reynoutria* spp.) invasion. *Biol. Invasions*, 10, 381–390.
- Tylianakis, J.M., Didham, R.K., Bascompte, J. & Wardle, D.A. (2008). Global change and species interactions in terrestrial ecosystems. *Ecol. Lett.*, 11, 1351–1363.
- Uetz, G.W. (1979). The influence of variation in litter habitats on spider communities. *Oecologia*, 40, 29–42.
- Vila, M., Espinar, J.L., Hejda, M., Hulme, P.E., Jarosik, V., Maron, J.L. et al. (2011). Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. *Ecol. Lett.*, 14, 702–708.
- Weidenhamer, J.D. & Callaway, R.M. (2010). Direct and indirect effects of invasive plants on soil chemistry and ecosystem function. *J. Chem. Ecol.*, 36, 59–69.
- Wolkovich, E.M., Bolger, D.T. & Holway, D.A. (2009). Complex responses to invasive grass litter by ground arthropods in a Mediterranean scrub ecosystem. *Oecologia*, 161, 697–708.
- Zavaleta, E.S., Pasari, J.R., Hulvey, K.B. & Tilman, G.D. (2010). Sustaining multiple ecosystem functions in grassland communities requires higher biodiversity. *Proc. Natl Acad. Sci.*, 107, 1443–1446.
- Zedler, J.B. & Kercher, S. (2004). Causes and consequences of invasive plants in wetlands: opportunities, opportunists, and outcomes. *Crit. Rev. Plant Sci.*, 23, 431–452.

SUPPORTING INFORMATION

Additional Supporting Information may be downloaded via the online version of this article at Wiley Online Library (www.ecologyletters.com).

Editor, Jessica Gurevitch

Manuscript received 20 October 2015

First decision made 19 November 2015

Manuscript accepted 26 November 2015