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INVITED REVIEW

Temperate forest termites: ecology, biogeography, and ecosystem impacts

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Abstract. 1. Wood decomposition in temperate forests is dominated by termites, fungi, and some species of ants and beetles. Outside of urban areas, temperate termite ecology is largely unknown, particularly when compared to tropical termites and other temperate organisms in the functional guild of wood-decomposing animals.

2. This review combines climate habitat modelling with knowledge of species physiology, behaviour, and community interactions to identify and prioritise future research on temperate termite ecology and biogeography.

3. Using a correlative climate model, the regional distributions of three common temperate forest termite species are shown to correlate with different aspects of climate (e.g. mean versus minimum monthly temperature), but that overall their distributions within temperate systems correlate more strongly with temperature variables than with precipitation variables.

4. Existing data are synthesised to outline how the subterranean, wood-nesting behaviour of most temperate forest termite species links their activity to an additional set of non-climate controls: wood type and tree species, soil depth, fungal activity, ant abundances and phenology, and competitive asymmetries among termite species.

5. Although fine-scale estimates of temperate termite abundances are rare, we provide upper bounds on their ecosystem impacts and illustrate how their regional abundances may influence forest structure and habitat availability for other organisms.

6. This review highlights that rigorous ecological studies in non-urban, intact ecosystems – with a particular focus on community interactions – are critically needed to accurately project future abundances, economic impacts, and ecosystem effects of temperate forest termites.

Key words. Biogeography, carbon cycling, *Coptotermes*, decomposition, fungi, Maxent, *Reticulitermes*, review, soil biodiversity, species distribution modeling.

Introduction

Soil animals influence a wide range of ecosystem properties and processes, including the productivity and composition of plant communities, soil structure and hydrology, nutrient availability, and organic matter decomposition (De Deyn *et al.,* 2003; Wardle *et al.,* 2004; Jouquet *et al.,* 2006; Wall *et al.,* 2008; Wickings & Grandy, 2011). Identifying the magnitude of these effects across landscapes is essential to understand global carbon and nutrient cycles (Wall *et al.,* 2008), yet this is precluded by insufficient data on species biomass and distributions across broad spatial scales (Fierer *et al.,* 2009; but see King *et al.,* 2013). These deficiencies appear especially applicable to soil macroinvertebrates (Fierer *et al.,* 2009), including termites, which have long been recognised as important species in many forested ecosystems (Brian, 1978). Indeed, Cornwell *et al.* (2009) suggested that termites deserve 'primary attention' in carbon-cycle models relative to other wood-decomposing animals owing to their potential to influence the fate of the estimated 72 Pg of carbon stored globally in dead wood (Pan *et al.,* 2011).

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Mention of termites commonly evokes images of tropical and sub-tropical ecosystems, yet termites are found in many temperate forests worldwide (Jones & Eggleton, 2011; Evans *et al.,* 2013). Much important research on temperate forest termites exists, but the majority has focused on control and eradication efforts – particularly in urban settings – owing to their large economic impacts (Su & Scheffrahn, 1990; Su, 2002). For example, in the United States (U.S.) termites are the most important structural pest with annual preventative and treatments costs of ~$2 billion USD (Suiter *et al.,* 2012). It is thus not surprising that the ecology and ecosystem impacts of termites in temperate systems have been somewhat overshadowed by an interest in mitigating their impacts as pests. However, their abundances in natural settings can be substantial (Howard *et al.,* 1982; Forschler & Townsend, 1996; Haverty *et al.,* 2000; King *et al.,* 2013) and their impacts on wood decomposition appear second only to wood-rot fungi in some temperate ecosystems (Bradford *et al.,* 2014).

The ecosystem impacts of tropical and savanna termites are relatively well documented and have been reviewed extensively (Abe *et al.,* 2000; Bignell, 2006; Bignell *et al.,* 2011). In contrast, efforts to quantify the abundances, regional distributions, and ecosystem effects of temperate forest termites are confounded by their largely subterranean nature and cryptic behavioural traits (Nutting & Jones, 1990; DeHeer & Vargo, 2004). As with tropical and savanna termites, temperate termites emit methane, fix nitrogen, modify soil properties, and alter forest structure and corresponding animal habitat availability by reducing the amount of standing and lying dead wood (Breznak *et al.,* 1973; Holt & Lepage, 2000; Geib *et al.,* 2008; Brune, 2010; Peterson, 2010; Evans, 2011; Jouquet *et al.,* 2011). The few existing estimates of the ecosystem impacts of temperate forest termites are based almost solely on extrapolations from studies in tropical, subtropical, and savanna ecosystems (e.g., Brian, 1978; Abe *et al.,* 2000), or through scaling up the effects of a few temperate termite species at local spatial scales (e.g. Fraser *et al.,* 1986; Sanderson, 1996).

In the present study, we synthesise current knowledge of the distributions and ecology of temperate forest termites. Owing to a paucity of data, we distill existing research into a series of questions, the answers to which should allow for robust estimates of temperate termite abundances and ecosystem process rates under current and changing environmental conditions. The paper consists of four sections. First, we describe the general classification and ecology of temperate forest termites, with the aim of facilitating cross-species synthesis. Second, we use an existing termite-occurrence database to model climate suitability of three dominant temperate termite species in the U.S. as a function of temperature and precipitation. Third, we explore how temperate termite ecology can be used to improve such estimates by identifying the dominant top-down and bottom-up ecological controls on temperate termite activity, all of which have the potential to decouple termite abundances from climate at regional scales. Last, we synthesise temperate termite impacts on forest structure and function, and we highlight why knowledge of their abundances is needed to project accurately current and future ecosystem function.

Classification of temperate forest termites

We define a 'temperate forest termite species' to be one that lives predominantly in a forested habitat located between 30° and 60° North or South latitude, with a climate classified as 'Temperate' (Group D) by the Köppen-Trewartha climate classification system (Belda *et al.,* 2014). The majority of termite species satisfying these criteria belong to the Rhinotermitidae, Kalotermitidae, Stolotermitidae, and Archotermopsidae families, with these last two families formerly placed within Termopsidae (Engel *et al.,* 2009; Lo & Eggleton, 2011). Temperate forest termites are generally either intermediate-type nesters (Rhinotermitidae; often referred to as 'subterranean' termites), where a colony nests and feeds in multiple pieces of wood that are connected by underground galleries; or single-piece nesters, where a single colony nests and feeds exclusively in a single piece of wood (typically 'dampwood' and 'drywood' termites in the Stolotermitidae, Archotermopsidae, and Kalotermitidae families) (Inward *et al.,* 2007). These life-history strategies contrast with the more diverse and evolutionarily recent 'higher' termites (Termitidae), which are generally separate-piece or soil nesters whose nests are distinct from the feeding sites (e.g. soil mounds). Higher termites are the dominant species in tropical and savanna ecosystems, and the ecology of many of these species is better understood than that of temperate termites. The temperate forest termite guild is thus largely representative of the evolutionary functional group known as 'lower termites', which are the dominant wood-decomposing animals in temperate forests worldwide and represent a key ecological unknown in wood-decomposition dynamics. As a starting point for synthesising temperate forest termite ecology and ecosystem impacts, we provide a list (Table S1, File S1) of temperate termite species and indicate the native and, where relevant, invaded geographical regions for each species.

Throughout this review we rely heavily on what is known about the ecology and distributions of *Reticulitermes flavipes* Kollar and *Coptotermes formosanus* Shiraki, as these two species are among the best-studied lower termites owing to their large economic impacts and global distributions (Table S1, File S1). Using these species we identify overarching trends that can improve our understanding of the ecology and distribution of other temperate termite species. The general lack of subterranean activity by singe-piece nesting termites precludes certain aspects of this review (e.g. tunnelling behaviour to avoid freezing) from pertaining to some species in the Stolotermitidae, Archotermopsidae, and Kalotermitidae families. However, temperate termites species otherwise share many ecosystem impacts (e.g. wood decomposition, methane production, etc.), biotic interactions (e.g. ant predation), and factors structuring their distributions (e.g. temperature and precipitation), thus enabling meaningful generalisations among the temperate forest termite guild.

Regional biogeography and climate

Globally, termite distributions correlate strongly with climate (Eggleton, 2000), yet the relative impact of different climate variables on temperate termite abundances is complex and species-specific (Haverty & Nutting, 1976; Houseman *et al.,* 2001; Fei & Henderson, 2004). Laboratory studies show that the activity of temperate forest termites responds to both temperature and moisture, but the relative importance of these variables in structuring distributions at the regional scale is unclear. An understanding of these broad-scale controls is particularly relevant for projecting current and future abundances, yet attempts to quantify regional distributions are hindered by a lack of systematic sampling and by the difficulty verifying termite presence or absence.

We used presence-only occurrence data of the three dominant termite species in eastern U.S. temperate forests (*R. flavipes, R. virginicus*, and *C. formosanus*) to investigate the extent to which their current distributions correlate with climate (Fig. 1; Table 1; see File S1 for the complete methods). We focus on modelling their distributions across the eastern U.S., yet an understanding of how climate structures their regional distributions is an important first step towards projecting their current and potential distributions worldwide. Termite-occurrence data were obtained from the National Termite Survey (NTS), which was started in 2002 to gather data on the distributions of termites in the U.S. (M. T. Messenger, pers. comm.). Portions of the data and the sampling methodology for the NTS have been published previously (Messenger *et al.,* 2002; Austin *et al.,* 2005, 2006, 2007; Szalanski *et al.,* 2006; Tripodi *et al.,* 2006; McKern *et al.,* 2007). Here, NTS city locations for *Reticulitermes flavipes, R. virginicus* and *Coptotermes formosanus* ($n = 771$) were batch digitised for georeferencing (GPS Visualizer, 2013) and 10% individually verified for accuracy (data are available in Table S2, File S1). These locations were used to create a presence-only species distribution model using a maximum entropy algorithm, Maxent 3.3.3a (Phillips *et al.,* 2006). Termite distributions were estimated using regional temperature and precipitation variables obtained from the WorldClim Version 1.4 data set (Hijmans *et al.,* 2005) and validated using published termite collection data (Table S3, File S1).

The results represent what we believe are the first model-based projections of species-specific climate suitability for temperate termites. Across all three species, temperature variables were stronger predictors of termite distributions than were precipitation variables (Table 1), yet the relative influence of each temperature variable differed among the species. *Reticulitermes flavipes* presence correlated most strongly with the mean annual temperature (accounting for 51% of the predictive power of the model), whereas the ranges of *R. virginicus* and *C. formosanus* correlated most strongly with the mean (39% and 25%, respectively) and minimum temperature (29% and 38%, respectively). The effect of precipitation was significantly less than that of temperature: *R. flavipes* presence correlated with annual precipitation (17%) and precipitation seasonality (14%), and *C. formosanus* presence correlated with precipitation of the wettest month (13.7%). Overall, climate suitability for *C. formosanus* was most predictable based on these climate variables [area under the curve (AUC) = 0.97], whereas climate suitability of *R. flavipes* was most difficult to predict (AUC = 0.78).

The model results provide a starting point for understanding the controls on temperate termite distributions, but there are several theoretical and practical issues that limit their broader applicability and interpretability. The NTS database is generally biased towards urban and suburban settings – which can provide altered moisture and temperature regimes – and it is, therefore, possible that the results reflect sampling intensity and bias as much as climate suitability (Merow *et al.,* 2013). To help overcome this practical limitation, the models were validated using data independent of the NTS that were collected without a known urban bias. Nevertheless, correlative models have inherent and well-documented limitations, particularly with regards to their ability to incorporate biotic interactions and non-climate related environmental controls (Phillips & Dudik, 2008; Fitzpatrick *et al.,* 2013; Merow *et al.,* 2013; Sax *et al.,* 2013). Thus, these model results must be interpreted alongside our current understanding of temperate termite ecology, in particular, the dominant biotic interactions and non-climate variables that structure their activity and survival.

Ecology

Temperate termites live in close association with other soil- and wood-inhabiting animals, and they experience an altered subterranean climate that can decouple species' responses from climate change (Cabrera & Kamble, 2001; Fridley *et al.,* 2011). We synthesise the current understanding of temperate forest termite physiology and ecology and identify non-climate factors that might serve as predominant controls on their distributions and abundances. The magnitude of these controls will be important to test and quantify further, especially since regional termite abundances largely determine the extent of their ecosystem impacts (Sanderson, 1996).

Abiotic variables

Temperate termites exhibit strikingly different distributions (e.g. Fig. 1), yet laboratory studies reveal that their physiological temperature tolerances can be quite similar, differing by only a few degrees for both the lower and upper lethal temperature limits (Sponsler & Appel, 1991; Hu & Appel, 2004). The discrepancy between physiological tolerances and geographical ranges suggests that temperate-termite geographical ranges do not necessarily depend on an individual termite's ability to survive at different temperatures. Instead, they also appear dependent on species-specific behavioural, physiological, and competitive adaptations that ensure whole colony survival under non-optimal temperatures.

One reason for the mismatch between the lethal temperature limits for different temperate termite species and their distributions might relate to the differing ability of subterranean termites to move vertically through the soil profile to regulate temperature (Houseman *et al.,* 2001). *Reticulitermes flavipes*, for example, can travel as deep as 1 m to avoid freezing temperatures (Cabrera & Kamble, 2001), perhaps explaining its more northerly range extent and the mismatch with its physiological tolerance. For some termite species (e.g. single piece nesters) the lack of deep subterranean galleries may preclude their survival at colder latitudes. The restricted distribution of *C. formosanus* compared with *R. flavipes* – in spite of their similar

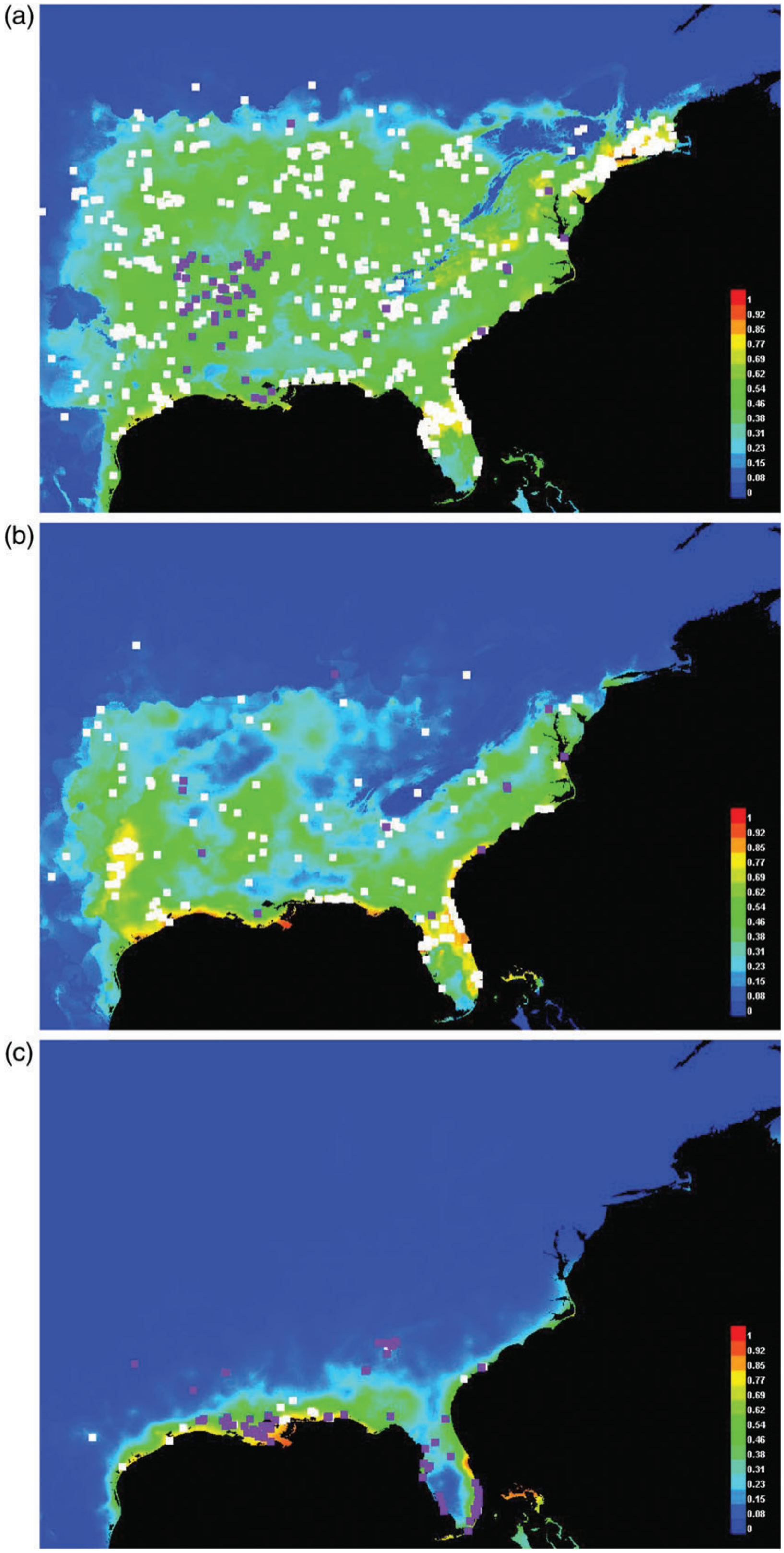

Fig. 1. Maxent-based predictions of climate suitability (1 = optimum habitat) across the eastern U.S. for (a) *Reticulitermes flavipes*, (b) *R. virginicus*, and (c) *Coptotermes formosanus*. White points show the locations of training data and purple points show the locations of test (validation) data. The predicted distribution for *R. flavipes* is the broadest and the hardest to predict based solely on climate variables (Table 2). *Coptotermes formosanus* has the smallest range of suitable habitat and it is strongly constrained by mean and minimum temperature. The range of suitable habitats and the predictive power of the model for *R. virginicus* were intermediate to both *R. flavipes* and *C. formosanus* (Table 2).

Table 1. Summary data from the Maxent models. Shown are the number of presence records used for training and testing each model. Percentage values for each climate variable represent the amount of model variation accounted for by that variable, with the mean across all three species given below each column. Performance was evaluated using the area under curve (AUC). The AUC gives the probability that a randomly chosen presence site is predicted to be a better fit by the model than a randomly chosen pseudo-absence site (Phillips & Dudik, 2008; see File S1). A random fit would have an AUC = 0.5, and a perfect fit would result in AUC = 1.0.

				Temperature (%)				Precipitation (%)			
Species	Train (N)	Test (N)	AUC (±SD)	*Mean*	*Max.*[*]	*Min.*[†]	*Var.*[‡]	*Mean*	*Max.*[*]	*Min.*[†]	*Var.*[§]
Reticulitermes flavipes	585	56	0.78 ± 0.02	50.9	8.2	3.7	4.4	17.3	1.3	0.7	13.5
Reticulitermes virginicus	137	13	0.81 ± 0.04	38.8	7.1	29.1	3.8	5.8	3.6	4.7	7.1
Coptotermes formosanus	22	88	0.97 ± 0.01	25.7	5.5	37.5	4.6	5.4	13.7	3.7	3.8
				38.5	6.9	23.4	4.3	9.5	6.2	3	8.1

[*] The maximum temperature/precipitation of the warmest/wettest month.
[†] The minimum temperature/precipitation of the coldest/driest month.
[‡] Annual temperature variance.
[§] Coefficient of variation of annual precipitation.

physiological tolerances – may in part reflect the inability of *C. formosanus* to over-winter at depth. Conversely, this species may simply have not yet reached its geographical limits (Pearson & Dawson, 2003). Such possibilities will only be answered with observations across time, or through experimental tests of whether species such as *C. formosanus* can survive northern winter temperatures if provided with deep enough soils.

Interactions between soil structure and precipitation may further disconnect termite abundances from climate variables. *Reticulitermes flavipes* is generally more active than other co-occurring termite species in shaded areas during cool moist months (Houseman *et al.,* 2001; Fei & Henderson, 2004), and can survive total submersion in water for nearly twice as long as *C. formosanus* individuals (20 vs. 11 h, respectively; Forschler & Henderson, 1995). *Reticulitermes flavipes* may therefore have a geographical advantage in the Northeastern U.S. region, where shallow soils lead to more saturated conditions, natural ponds, and ephemeral water bodies than in the Southeastern U.S. (with the exception of peninsular Florida; Zedler, 2003). Abiotic factors such as soil depth may then modify climate- or physiological-based inferences of habitat suitability because behavioural differences among species influence the translation of their physiology into their realised abundances.

Biotic variables

There is strong evidence that temperate termite abundances, distributions, and ecosystem impacts depend on a multitude of top-down and bottom-up interactions, including ant predation, presence of wood-rot fungi, and wood quality and type. As with temperate termites, these factors are also affected by abiotic conditions, thus complicating efforts to identify the dominant controls on termite distributions using only physiological or correlative data. An understanding of how these biotic interactions structure regional termite distributions is thus integral for accurately modelling termite abundances and corresponding ecosystem impacts.

Bottom-up controls. Temperate termites live in close association with dead wood. Their activity is thus influenced by a suite of wood traits, which potentially link their regional abundances to tree species distributions. Wood traits vary substantially across climate gradients, and what appear to be climate-related controls on termite abundances may instead be the result of termite preferences for specific tree species or wood traits. Indeed, wood-eating termites typically select wood that requires less energy to consume (Peralta *et al.,* 2004), and softer wood may allow for higher termite abundances by yielding more net energy per gramme of wood consumed. Laboratory studies show that temperate termites often prefer gymnosperm wood over angiosperm wood (Smythe & Carter, 1969; Waller & La Fage, 1987; Waller, 1988; Waller *et al.,* 1990), with gymnosperms generally being less dense than angiosperms (Weedon *et al.,* 2009). Termites in some regions may, therefore, be constrained by lower-quality food sources. For example, according to the Janka hardness scale (Behr *et al.,* 1972; Green *et al.,* 2006), the top five most abundant tree species in the Northeastern U.S. (*Acer rubrum, Acer saccharum, Fraxinus americana, Fagus grandifolia*, and *Prunus serotina*) are ~50% harder than the top five most abundant tree species in the Southeastern U.S. (*Pinus taeda, Acer rubrum, Liquidambar straciflua, Pinus elliotti*, and *Liriodendron tuliperfia*) (compiled from Ross, 2010; Prasad *et al.,* 2012). Termites in the Northeastern U.S. may experience low-quality food sources relative to other regions, which may in turn limit termite abundances or select for species that can persist in more stressful habitats. Uncertainty over the relative importance of various wood traits in dictating termite activity and survival currently limits our ability to project how these trends structure regional temperate termite abundances.

Temperate termite activity also depends on the type and amount of wood-inhabiting fungi present in dead wood. As with tree species, fungal species and fungal traits vary substantially across climate and latitudinal gradients, with brown-rot fungi proportionally more abundant in cold, dry regions and white-rot fungi more abundant in moist, warm regions (Stokland *et al.,* 2012). Temperate termite species often show a preference for wood colonised by brown-rot fungi (Lenz *et al.,* 1980, 1991; Ruyooka & Edwards, 1980; Getty & Haverty, 1998; Suarez & Thorne, 2000), and there is some evidence that *C. formosanus* is less able to consume fungal-colonised wood than *R. flavipes* (Lenz *et al.,* 1991), perhaps facilitating a broader

Table 2. Ecosystem process rates by various temperate termite species. Wood consumption rates depend upon moisture and water availability (Khan, 1980), temperature (Lenz *et al.,* 1983), wood type (Lenz *et al.,* 1983; Ripa *et al.,* 2002), fungal activity (Lenz *et al.,* 1991), and wood quantity (Cornelius & Osbrink, 2001), thus complicating efforts to extrapolate laboratory estimates to the ecosystem level (Lenz *et al.,* 1983). Methane production rates vary drastically between species and depend predominantly upon the assay temperature (Fraser *et al.,* 1986). Nitrogen fixation rates may depend upon the N availability in wood (Meuti *et al.,* 2010), temperature and caste ratio (Breznak *et al.,* 1973; Curtis & Waller, 1998).

Ecosystem effect (*species*)	Rate	Notes	Reference
Wood consumption			
C. formosanus	48–78 mg g^{-1} day^{-1}	Depended upon size of wood block	Cornelius and Osbrink (2001)
P. adamsoni	11.6–26.7 mg g^{-1} day^{-1}	Depended upon percent decayed by fungi and wood type	Lenz *et al.* (1991)
P. adamsoni	4–35 mg g^{-1} day^{-1}	Increased as temperature increased from 8 to 26 °C	Lenz *et al.* (1983)
R. flavipes	36–51 mg g^{-1} day^{-1}	Depended upon size of wood block	Cornelius and Osbrink (2001)
R. flavipes	22–50 mg g^{-1} day^{-1}	Depended upon per cent decayed by fungi and wood type	Lenz *et al.* (1991)
R. flavipes	45–51 mg g^{-1} day^{-1}	Depended upon wood species and moisture content	Tai and Wu (2003)
Reticulitermes spp.	30–39 mg g^{-1} day^{-1}	Depended upon wood species	Ripa *et al.* (2002)
Methane production			
C. formosanus	1.4 mg CH_4 kg^{-1} day^{-1}	Production rate at 26 °C	Fraser *et al.* (1986)
C. formosanus	26.9 mg CH_4 kg^{-1} day^{-1}[*]	Production rate at 25 °C	Wheeler *et al.* (1996)
R. flavipes	9.6 mg CH_4 kg^{-1} day^{-1}	Production rate at 26 °C	Fraser *et al.* (1986)
R. flavipes	36.0 mg CH_4 kg^{-1} day^{-1}[†]	Production rate at 23 °C	Odelson and Breznak (1983)
R. flavipes	96.0 mg CH_4 kg^{-1} day^{-1}[*]	Production rate at 25 °C	Wheeler *et al.* (1996)
R. tibialis	79.2 mg CH_4 kg^{-1} day^{-1}	Production rate at 26 °C	Fraser *et al.* (1986)
Z. angusticollis	153.6 mg CH_4 kg^{-1} day^{-1}[*]	Production rate at 25 °C	Wheeler *et al.* (1996)
Z. angusticollis	84.0 mg CH_4 kg^{-1} day^{-1}	Production rate at 26 °C	Fraser *et al.* (1986)
Z. nevadensis	156.0 mg CH_4 kg^{-1} day^{-1}[‡]	Production rate at 20 °C	Zimmerman and Greenberg (1983)
Nitrogen fixation			
C. formosanus	1.3–6.5 μg N_2 g^{-1} day^{-1}[§]	Differed between soldier and worker (highest in workers)	Breznak *et al.* (1973)
R. flavipes	0.7–2.0 μg N_2 g^{-1} day^{-1}[§]	Differed between soldier and worker (highest in workers)	Breznak *et al.* (1973)
R. lucifugus	8.4 μg N_2 g^{-1} day^{-1}[§]	Aerobic conditions	Golichenkov et al. (2002)
Reticulitermes spp.	2.8–9.9 μg N_2 g^{-1} day^{-1}[§]	Decreased over measurement period; depended on colony	Pandey *et al.* (1992)
Reticulitermes spp.	0.5–3.5 μg N_2 g^{-1} day^{-1}[¶]	Varied seasonally, with lower rates in colder temperatures; depended on caste proportion (e.g., workers vs. soldiers)	Curtis and Waller (1998)
Z. angusticollis	52.3 μg N_2 g^{-1} day^{-1}[§]	Aerobic conditions	Golichenkov *et al.* (2002)
Zootermopsis spp.	2.5 μg N_2 g^{-1} day^{-1}[§]	Only included reproductive nymphs and workers	Breznak *et al.* (1973)

[*] Visually estimated from Figure 5 in Wheeler *et al.* (1996).
[†] Calculated using their reported fresh weight of 4.0 mg per termite.
[‡] Calculated using a fresh weight of 50 mg per termite as in Fraser *et al.* (1986).
[§] Converted from reported C_2H_4 production (via acetylene reduction) using the theoretical ratio of 3 : 1 as suggested in Bentley (1984) and Curtis and Waller (1998).
[¶] Visually estimated from Figure 1 in Curtis and Waller (1998).

geographical distribution for *R. flavipes.* However, our current understanding of termite-fungus interactions is limited – largely due to a lack of *in situ* studies – and such relationships probably depend on the specific termite, fungus, and tree species involved (e.g. Lenz *et al.,* 1991; Kirker *et al.,* 2012). Further, many fungi have strong tree host preferences, making it difficult to disentangle the relative impact of climate, wood traits, and fungal traits on termite survival and abundance. Resolving uncertainty about how wood-rot fungi and wood characteristics interact to influence termite performance in temperate forests is essential for projecting how temperate termite abundances will respond to a variety of forest disturbances.

Top-down controls. Top-down control on termites is thought to be dominated by ant predation (Eggleton, 2011). In the eastern U.S., several native and invasive woodland ant species prey on termites (Beard, 1973; Shelton *et al.,* 2003; Bednar & Silverman, 2011). Of these, ants in the *Aphaenogaster rudis* complex are among the most ubiquitously distributed and abundant (King *et al.,* 2013). Ants can inflict 100% mortality on exposed termites (Buczkowski & Bennett, 2007, 2008), reduce termite colonisation rates of dead wood by over 90% (Beard, 1974), and limit total wood decomposition rates by ~10% when both guilds are present in the same piece of woody debris (Warren & Bradford, 2012).

Given the potential for strong top-down control by ants, it therefore seems somewhat paradoxical that termite abundances correlate strongly with ant abundances across eastern U.S. temperate forests (King *et al.,* 2013). However, differences between ant and termite phenologies (i.e. seasonal foraging windows) may explain this paradox by providing termites in warmer regions with longer ant-free foraging windows. For example, *R. flavipes* can remain active at temperatures above 3.7 °C (Hu & Appel, 2004), whereas *A. picea* (the more northerly distributed *Aphaenogaster* spp. in the eastern U.S.) and *A. rudis* (the more southerly *Aphaenogaster* spp.) are active at temperatures above 4 and 10 °C, respectively (Warren *et al.,* 2011). Using average daily temperatures obtained from the National Climate Data Center over the past 18 years (National Climate Data Center, 2013), we calculated that these differences in phenology result in an average of 3 days annually where temperatures allow for foraging by *R. flavipes* but limit foraging by *Aphaenogaster* spp. In contrast, *R. flavipes* experiences an estimated 59 'ant-free' foraging days annually in Georgia. These ant-free foraging days comprise 1.3% (3 of 259) and 17.5% (59 of 340) of the species' annual foraging days in the Northeast and Southeast, respectively. Thus, it may not be colder temperatures *per se* that limit termite abundances, but rather the fact that colder temperatures in the Northeast induce a close synchrony between ant and termite phenologies.

Although ants are undoubtedly the best-studied predators of temperate termites, other soil-dwelling animals have been shown to influence termite survival rates and activity. For example, the red-backed salamander, *Plethodon cinereus* (Green), also exhibits a strong feeding preference for *Reticulitermes* spp. in laboratory studies (Gabor & Jaeger, 1995). Similarly, Beard (1974) gives anecdotal evidence that centipedes prey on termites in controlled settings, but notes that field colonies still thrive in their presence. As with ants, the extent and magnitude of top-down control by these soil-dwelling animals remains largely unknown. Improving our understanding of these trophic interactions is integral for disentangling the relative impact of climate versus biotic interactions on temperate forest termite abundances and ecosystem impacts.

Competition. Behavioural and physiological differences among temperate termite species can affect wood consumption and colonisation rates (Su & Scheffrahn, 1988; Cornelius & Osbrink, 2001), potentially facilitating niche differentiation and thus structuring regional termite abundances. For example, higher survival and wood consumption rates by *R. flavipes* at colder temperatures relative to *C. formosanus* (Smythe & Williams, 1972; Hu & Song, 2007) may allow several additional weeks of activity in the spring and fall by *R. flavipes*. Conversely, higher survival and wood consumption rates by *C. formosanus* at warmer temperatures is likely to give this species a competitive advantage in warmer latitudes. Temperate termites may therefore have similar physiological tolerances, food requirements, and predators, but different temperature optima may determine colony abundances and range boundaries in regions where species co-occur.

Temperate termite abundances are also influenced by inter- and intra-specific antagonism among termite species (Perdereau *et al.,* 2011). In marginal or newly-invaded habitats, species survival is maximised when a species can outcompete co-occurring termites while minimising aggression between colonies of the same species. This 'competitive asymmetry' is likely to facilitate invasive termites becoming competitively dominant by limiting the amount of self-inflicted mortality between conspecifics (Perdereau *et al.,* 2011). Indeed, *R. flavipes* and *C. formosanus* – both invasive in many parts of the world (Table S1, File S1) – display high levels of inter-specific antagonism and low levels of intra-specific antagonism (Su & Scheffrahn, 1988; Bulmer & Traniello, 2002; Vargo & Husseneder, 2009; Perdereau *et al.,* 2011). Low levels of intra-specific aggression may also provide some termite species with an evolutionary advantage in areas with poor habitat by minimising energy lost in competitive interactions. A better understanding of the evolutionary and ecological tradeoffs among high and low intra- and inter-specific competition is particularly relevant for identifying which species are likely to persist in novel habitats or expand their range boundaries as the climate changes.

Ecosystem effects

Knowledge of the controls on temperate termite distributions and abundances is not only valuable from an ecological perspective, but also from an applied perspective. Subterranean termites substantially alter forest structure and function, with the magnitude of these effects strongly determined by their regional abundances (Sanderson, 1996). Precise estimates of temperate termites' ecosystem impacts are currently precluded by a lack of regional abundance data; we, therefore, synthesise existing ecosystem process rates to place upper bounds on their ecosystem effects and to prioritise future research.

Temperate termites impact forest structure and function in a multitude of ways (Tables 2 and 3), with wood decomposition being the dominant process. Dead wood constitutes 5–10% (36–72 Pg) of the world's terrestrial carbon store (Cornwell *et al.,* 2009; Weedon *et al.,* 2009; Pan *et al.,* 2011), and the extent to which wood-decomposing invertebrates respond to climate change has important implications for the global carbon cycle (Cornwell *et al.,* 2009). Invertebrates affect wood decomposition rates directly, by feeding on wood, and indirectly, by altering the activity and composition of wood-decaying fungi (Crowther *et al.,* 2011, 2012). Termite-mediated wood decomposition rates generally increase with increasing temperature (Lenz *et al.,* 1983), highlighting the potential for climate-driven feedback loops.

Estimates of wood decomposition rates for temperate termites in laboratory settings are common (Table 2), yet there are surprisingly few *in situ* estimates for any temperate termite species. Using recently published regional termite biomass estimates across the eastern U.S. (King *et al.,* 2013) and an approximate maximum wood decomposition rate of 50 mg g-termite^{-1} day^{-1} for *R. flavipes* (Table 2), we estimate that *Reticulitermes* spp. consume between 0 and 0.017 Mg-wood ha^{-1} year^{-1} in U.S. forests. This wood consumption represents 10% of annual dead wood biomass inputs in some eastern deciduous forests (Harmon *et al.,* 1986) and closely aligns with one of the few field estimates of 3–12% annual termite-mediated mass loss (Gentry & Whitford, 1982). However, given the high spatial heterogeneity of termite abundances and the unreliability of laboratory-based wood-decomposition rates (Lenz *et al.,* 1983) *in situ* estimates of temperate termite wood decomposition rates remain a research priority (Table 3).

Table 3. Community and ecosystem effects of temperate termites. In contrast to many tropical and savanna termites, the impacts of temperate termites on these aspects of forest structure and function remain largely unquantified. Estimates of process rates exist for many of these effects (Table 2), but a lack of *in situ* studies and limited termite biomass data preclude attempts to estimate regional-scale impacts or to extrapolate to novel habitats.

Ecosystem effect	Reference
Soil	
Rate of mixing between soil horizons	Peterson (2010)
Effects on water infiltration	Peterson (2010)
Translocation of soil into wood	Nutting *et al.* (1987)
Changes in soil chemical concentrations	Holt and Lepage (2000)
Changes in soil bulk density	Peterson (2010)
Changes in soil organic carbon fraction	Holt and Lepage (2000)
Nitrogen	
Increase N fixation in N poor environments	Meuti *et al.* (2010)
Effects of N fixation on microbial activity and biomass	Chouvenc *et al.* (2008)
Regional N fixation rates	Peterson (2010)
Wood decomposition	
Decomposition rates of buried wood	Li and Su (2008)
Effects on lignin degradation	Geib *et al.* (2008)
Regional decomposition rates	Bradford *et al.* (2014)
Wood decomposition dynamics	
Inhibition of fungal growth and biomass in wood	Hamilton and Bulmer (2012)
Methane	
In situ methane production rates	–
Forest structure	
Impacts on snag decomposition and felling rates	Keen (1929)
Impact on density and viability of nurse logs	–

Many temperate termite species also produce methane and fix atmospheric nitrogen via symbiotic microorganisms in their hindgut (Table 2; Breznak *et al.,* 1973; Brune, 2010); however, it appears that regional termite production rates of both these gases are negligible relative to non-termite sources. Recent estimates of total methane emissions by termites in temperate ecosystems are between 0.02 and 0.09 Tg year^{-1} (Fraser *et al.,* 1986; Sanderson, 1996; Sugimoto *et al.*, 1998), which are dwarfed by emissions from anthropogenic sources of more than 600 Tg year^{-1} (Brune, 2010). Regional-scale estimates of nitrogen fixation rates by *Reticulitermes* spp. are as high as 0.5 kg N ha^{-1} year^{-1} (Pandey *et al.,* 1992), but are most likely <0.01 kg N ha^{-1} year^{-1}, assuming a maximum nitrogen-fixation rate of 10 μg N$_2$ g^{-1} day^{-1} (Table 2) and a maximum density of 910 g-termite ha^{-1} (King *et al.,* 2013). These rates are an order of magnitude less than non-termite-mediated nitrogen fluxes, which total between 6.5 and 26.6 kg N ha^{-1} year^{-1} in temperate forests globally (Cleveland *et al.,* 1999). Temperate termites do, however, deposit substantial amounts of nitrogen in individual logs (Curtis & Waller, 1998), which may alter wood decomposition rates of saprotrophic fungi (Knorr *et al.,* 2005; Boberg *et al.,* 2008).

Some of the most interesting – yet least explored – questions regarding the ecosystem impacts of temperate termites centre on how they affect soils (Table 3). Termites are often labelled as 'ecosystem engineers', in part due to their extensive impacts on soil structure and chemistry (Bignell, 2006; Jouquet *et al.,* 2006). The effects of mound-building termites on soil properties have received the bulk of attention in this area, yet subterranean temperate termites undoubtedly have numerous undocumented impacts on soil properties (Peterson, 2010). Termites alter the structure and chemistry of soils through tunnelling, soil translocation, deposition of organic matter (saliva and faeces), and by influencing the form of wood-bound-carbon that is made available to soil organisms (i.e. lignin vs. cellulose) (Holt & Lepage, 2000). Owing to the enormous differences in behaviour between intermediate/single-piece nesters and separate-piece nesters, our ability to use data from separate-piece nesting termites (e.g. mound builders) to predict how subterranean termites alter soils is severely limited. More research into how temperate termites affect soil properties is thus needed to quantify the full range of ecosystem impacts of these ecosystem engineers.

In addition to altering biogeochemical cycles and soil properties, termite-mediated decomposition of snags (standing dead trees) and stumps can alter densities of birds, bats, mammals, arthropods, and tree seedlings, many of which rely on these woody structures for habitat and as nurse logs (Harmon *et al.,* 1986; Evans, 2011). Indeed, the integral role that temperate termites play in decomposing snags has been recognised for nearly 100 years (Snyder, 1915; Keen, 1929). Using Forest Inventory and Analysis (FIA) data from the U.S. Forest Service (http://www.fia.fs.fed.us/) we show that termite densities correlate with the upper bound of standing dead wood densities in forests (Fig. 2). FIA data further reveal that snag densities in eastern U.S. forests generally decrease with decreasing latitude, with an average of 47.6 snags per ha in eastern states >40°N latitude, 26.3 snags per ha in states between 35°N and 40°N latitude, and 18.7 snags per ha in states <35°N latitude (see File S1 for details). These regional snag densities inversely correlate with estimates of regional termite biomass in temperate forests (King *et al.,* 2013). Such latitudinal trends are undoubtedly influenced by differences in forest type, live tree densities, climate, and management strategies across this regional gradient, but it is possible that termites play a role in changing forest structure and habitat availability by altering the density of standing dead trees.

Conclusions

Our synthesis is intended to identify knowledge gaps regarding the controls on temperate termite abundances and distributions, and to put into perspective why an understanding of their abundances is needed to project forest structure and function accurately. A key conclusion is that the lack of data on the ecology of termites in temperate forests is a barrier to generalised, major conceptual advances for this insect guild. Thus, we must emphasise the critical need for further study of these species in non-urban, intact ecosystems, with a particular focus on their

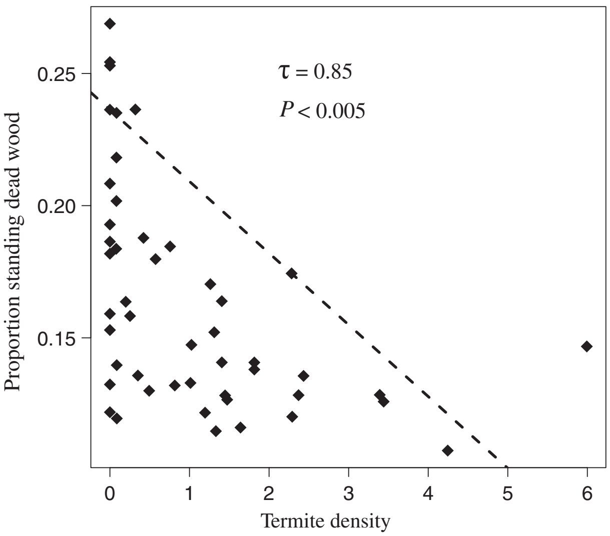

Fig. 2. Termite densities for each state in the U.S. correlate with the upper bound of the proportion of standing dead wood. The dashed line is the '85th percentile quantile regression line', which predicts the maximum value that is, on average, greater than 85% of the observed values at a given termite density. Owing to non-uniform variation, quantile regression – which can predict the upper bound rather than the mean – was used in place of standard linear regression (*see* Cade & Noon, 2003). 'Proportion standing dead wood' was calculated as: (density standing dead wood) × (density standing dead wood + density live wood)$^{-1}$. Termite density for each state was estimated by dividing the number of cities with termite occurrences by the log of the terrestrial area of that state (see File S1 for full methods).

community interactions. We show that climate variables correlate with known temperate termite distributions in the eastern U.S., but our synthesis suggests that biotic and soil characteristics may be equally or more important for structuring local and regional termite abundances. Specifically, termite distributions appear controlled by several important biotic and environmental interactions, namely: tree species and wood traits, fungal preferences and colonisation, soil depth, phenology of predatory ants, and competitive asymmetries among coexisting termite species.

Improving our understanding of the ecology of temperate termites is needed to: (i) obtain realistic estimates of termite abundances and corresponding ecosystem effects, both locally and regionally; (ii) project how termite abundances and ecosystem impacts will respond to environmental change; (iii) predict the relative success or failure of temperate termites in non-native habitats; and (iv) estimate termite-mediated ecosystem effects at the regional scale in order to improve the robustness of carbon and nitrogen budgets. The relative influence of biotic and abiotic factors on temperate termite distributions remains unknown, and these factors will ultimately determine future abundances, economic impacts, and ecosystem effects of temperate forest termites.

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Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: 10.1111/een.12185

File S1. Compilation of common temperate forest termite species (Table S1), full methods and data for the Maxent model (Tables S2-S3), and detailed methods for the quantile regression model.

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