

LETTER

Phenological response of a key ecosystem function to biological invasion

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Abstract

Although climate warming has been widely demonstrated to induce shifts in the timing of many biological events, the phenological consequences of other prominent global change drivers remain largely unknown. Here, we investigated the effects of biological invasions on the seasonality of leaf litter decomposition, a crucial freshwater ecosystem function. Decomposition rates were quantified in 18 temperate shallow lakes distributed along a gradient of crayfish invasion and a temperature-based model was constructed to predict yearly patterns of decomposition. We found that, through direct detritus consumption, omnivorous invasive crayfish accelerated decomposition rates up to fivefold in spring, enhancing temperature dependence of the process and shortening the period of major detritus availability in the ecosystem by up to 39 days (95% CI: 15–61). The fact that our estimates are an order of magnitude higher than any previously reported climate-driven phenological shifts indicates that some powerful drivers of phenological change have been largely overlooked.

Keywords

Detritus, ecosystem process, invasive species, leaf litter decomposition, metabolic theory of ecology, non-native crayfish, seasonality, shallow lakes.

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INTRODUCTION

Recent studies have demonstrated that climate warming can induce changes in the timing of many biological events such as earlier flowering of plants or shifted timing of bird and salmon migrations (Walther *et al.* 2002; Cleland *et al.* 2007). Such phenological shifts may result in dramatic propagating effects across levels of biological organisation through modifying population dynamics and the synchrony of species interactions (Edwards & Richardson 2004; Winder & Schindler 2004). While human-driven global change comprises many major processes other than climate warming, there is hardly any evidence to date of non-climate driven phenological shifts (Cleland *et al.* 2007; Thackeray *et al.* 2010). Biological invasions are a pervasive component of global change that affects virtually all ecosystems worldwide, causing strong economical and ecological impacts (Simberloff *et al.* 2013). Following their initial introduction, the success of invaders is often driven by the fact that they display different and more plastic phenological traits than native species (Stachowicz & Tilman 2005; Wolkovich & Cleland 2010). When invaders become highly abundant in the recipient ecosystems, they may therefore induce strong phenological shifts on available resources, competitors and/or predators and such invasion-driven shifts likely modify temporal patterns of ecosystem processes.

In its traditional definition, phenology describes the timing of an organism's life cycle events such as the onset of the reproductive period, migration, metamorphosis and senescence (Schwartz 2003); death has been typically considered as the ultimate stage of phenology. However, the effect of an organism on an ecosystem extends beyond its death through the

detritus stage (Odling-Smee *et al.* 2003), which should thus be considered when studying phenology of ecosystem processes. Detritus is an ubiquitous form of energy and a major determinant of biodiversity and ecosystem stability (Moore *et al.* 2004; Rooney & McCann 2012). The timing at which 'primary' detritus (i.e. animal carcasses, plant litter) and its derivatives upon decomposition are delivered to and disappear from ecosystems can strongly influence not only the life history and demography of decomposers (Cummins *et al.* 1989) but also the structure of detrital food webs, and ultimately temporal patterns of ecosystem functioning. This consideration is in line with the fact that the concept of phenology is being increasingly applied to many processes occurring at the ecosystem level, e.g. biogeochemical cycles (Noormets 2009). It thus provides rationale for extending the notion of 'living phenology' to 'phenology of detritus' that reflects temporal patterns of detritus presence in an ecosystem which are tightly linked to phenology of some key ecosystem processes (e.g. carbon and nutrient cycling).

Here, we tested whether and how invasive omnivorous crayfish modify detritus phenology in temperate lakes and quantified the intensity of this shift. Being omnivorous, freshwater crayfish can increase leaf litter decomposition rates by direct consumption of litter or decrease them through predation on other detritivores (e.g. Usio 2000; Dunoyer *et al.* 2014). Several crayfish species have become highly successful invaders in freshwater habitats worldwide (Strayer 2010), inducing strong ecological impacts (Twardochleb *et al.* 2013) especially where native crayfish are naturally lacking (Rodriguez *et al.* 2003). We quantified the direct and indirect effects of an invasive crayfish on litter decomposition in 18 shallow lakes along a

pronounced gradient of crayfish invasion. Rates of decomposition assessed at two seasons were used to reconstruct yearly patterns of detritus standing stock in the study lakes using a temperature-based model. We tested the prediction that decomposition rates would increase and the period of leaf detritus availability would be shortened in invaded lakes, the effect scaling positively with increasing crayfish invasion intensity.

MATERIAL AND METHODS

Study sites

The study was conducted in 18 shallow lakes of gravel-pit origin situated in the Garonne river catchment in southwest France (Supporting Information, SI 1). Among five freshwater crayfish native to Europe, three are found in France, however, none of them occurs in lakes in the region, where the experiment was conducted (Collas *et al.* 2007). The study lakes thus lacked native crayfish, but two non-native species, the red-swamp crayfish (*Procambarus clarkia*, Girard) and spiny-cheek crayfish (*Orconectes limosus*, Rafinesque), were present. Originating from North America, both species were successfully introduced in Europe since the late 19th century (Hobbs *et al.* 1989) and detritus is an important food source for both (Gutierrez-Yurrita *et al.* 1998; Vojtkovska *et al.* 2014).

The study lakes were selected to include a wide range of crayfish invasion. Invasion intensity was assessed at two sampling occasions and was expressed as the total biomass of crayfish captured per unit effort (Supporting Information, SI 2). Adult *Procambarus clarki* dominated total crayfish biomass in all lakes except one moderately invaded lake where *Orconectes limosus* was co-dominant (Table S3). While crayfish presence was detected in all lakes, difference in their biomass between the least and the most invaded lakes was striking, ranging from 1.6 to 536.1 g trap⁻¹ night⁻¹. No single biotic or abiotic predictor of this variation has been identified (Table S4) and it is thus thought to primarily reflect the variable success and different stages of invasion across the lakes. Importantly there was no significant correlation of crayfish biomass with neither nutrient availability nor riparian tree cover, which could directly affect litter decomposition (Table S4).

Litter decomposition

Abscised leaves of black poplar (*Populus nigra*), the dominant riparian tree of the study lakes (40–96% of riparian vegetation; Supporting Information, SI 1), were collected at a single location during autumn leaf fall in October and November 2013. The leaf litter was air-dried for storage and mass determination (nearest 0.01 g). Packs of three grams of air-dried leaves were exposed to decomposers in the littoral zone of each lake. Total decomposition rate was assessed based on the mass loss of unconfined leaf packs (leaves bound at their stalks with a fine annealed wire). To differentiate the contribution of crayfish and small invertebrate detritivores to

decomposition, additional leaf packs were exposed confined in coarse mesh bags made of 5-mm square mesh plastic fence to exclude crayfish but allow other invertebrates and microbes to access the leaves. Lastly, leaf packs exposed in fine mesh bags made of 500 µm mesh nylon net were used to assess the mass loss driven primarily by microbial activity and leaching.

Litter decomposition rates were first assessed in winter (November 2013–January 2014), a time at which lakes in the region were replenished with leaf litter from riparian trees and water temperature was at its yearly minimum (mean water temperature: 7.8 °C ± 0.3 SD). A second decomposition experiment was performed in mid-spring (April–May 2014), a warmer period (mean water temperature: 18.3 °C ± 0.42 SD) when a large part of leaf litter stock was still available. The red swamp crayfish (*Procambarus clarkii*), comprising 94% of crayfish biomass in the study lakes, has been reported to have a preference for temperatures between 22 and 26 °C (Espina *et al.* 1993), while being nearly inactive below 10 °C (Croll & Watts 2004), thus we expected a seasonal difference in their effect on litter decomposition. Experiment duration (77 and 35 days in winter and spring respectively) was determined to capture mid-stage decomposition of unconfined leaf packs (ca. 50% litter dry mass remaining) and to obtain similar sums of degree-days (i.e. 596 and 637 degree-days in winter and spring respectively).

Four replicates of each leaf pack type were placed in each lake at each season, resulting in a total of 432 leaf packs deployed in the field. Exposure sites were spaced at least 100 m apart and their exact shoreline positions were selected to capture within-lake variability in littoral zone morphology. At each site, a set of the three different types of leaf packs (namely unconfined, confined in coarse mesh bags and confined in fine mesh bags) was anchored along a one-meter iron rebar wedged into the bottom at a depth of ca. 0.6–1 m. Water temperature in the littoral zone was recorded hourly by temperature loggers (HOBO Temperature/Light Data Logger UA-002-64; Onset Computer Corporation, Bourne, MA, USA) attached to the iron rebar at one randomly selected site per lake. At the end of the litter exposure time, leaf packs were retrieved, placed individually in plastic bags, transported to the laboratory in a cooler and stored at –20 °C until processing. In the laboratory, leaves were carefully rinsed, oven dried at 70 °C for 72 h and weighed to the nearest 0.01 g.

Daily decomposition rate (k) was calculated as follows:

$$k = \frac{-\ln(X)}{t} \quad (1)$$

where X is the proportion of litter mass remaining calculated as the ratio of final (M_f) to initial (M_i) oven-dried mass of leaf litter and t is the exposure time (days) (Lecerf *et al.* 2005). M_i was estimated based on the relationship between air-dry and oven-dried leaf litter mass established using eight extra leaf packs oven-dried for 72 h after measurement of air-dry mass. The percent contribution of crayfish, invertebrate detritivores and microbial decomposers to litter mass loss was determined assuming additive effects (Handa *et al.* 2014):

$$\% \text{ crayfish} = \frac{(Y_{UL} - Y_{CM}) \times 100}{Y_{UL}} \quad (2)$$

$$\% \text{ detritivore} = \frac{(Y_{CM} - Y_{FM}) \times 100}{Y_{UL}} \quad (3)$$

$$\% \text{ microbial} = \frac{Y_{FM} \times 100}{Y_{UL}} - \% \text{ leaching} \quad (4)$$

where Y is the proportional mass loss in unconfined leaf litter (Y_{UL}) and of leaf litter enclosed in coarse (Y_{CM}) and fine (Y_{FM}) mesh bags. Percent microbial contribution was corrected for litter mass loss due to leaching determined for 48 h in a controlled laboratory experiment at +8 °C and +18 °C (i.e. mean temperatures in the study lakes observed in winter and spring respectively). Leaching accounted for $11.0\% \pm 0.56$ SE and $13.5\% \pm 0.41$ SE of litter mass loss at +8 °C and +18 °C respectively.

Statistical analyses and modelling

A linear mixed-effects model was used to compare the rates of litter decomposition assessed under the different modalities of litter exposure (unconfined leaf litter packs vs. coarse mesh bags vs. fine mesh bags) at two seasons and to estimate spatial variance components (between and within lakes). We found that within lake variation was negligible (< 1%; Supporting Information, SI 3) and most of the variance in litter decomposition rate was accounted for by Leaf pack type, Season and their interaction (Table S6). Subsequent statistical analyses were therefore performed using data averaged across sites. Analysis of covariance (ANCOVA) was used to examine main and interactive effects of Invasion intensity and Season on decomposition rates for each leaf pack type, and the percent contribution of crayfish, invertebrate detritivores and microbial decomposers to total decomposition. Model assumptions were evaluated based on diagnostic graphs and, when necessary, response variables were ln-transformed. Statistics were performed in R using packages *base* and *nlme* (R Core Team 2013; Pinheiro *et al.* 2015).

A heuristic model of litter decomposition was built to predict the proportion of litter mass remaining as a function of water temperature and time elapsed since leaf fall into the lakes. To limit model complexity, we assumed (1) total leaf inputs into lakes to occur at a single event, corresponding to the day of the first autumnal frost, (2) leaf litter standing stock to consist of black poplar leaves and (3) the key temporally variable environmental parameter that drives leaf litter decomposition to be temperature and its correlates. The first two assumptions were consistent with the fact that most litter delivery to fresh waters in temperate regions occurs during autumn leaf fall and black poplar is the main tree species in riparian zones in the study area (Supporting Information, SI 1). The third assumption was based on the metabolic theory of ecology (MTE) predicting a universal temperature dependence of any biological process rate related to metabolism (Brown *et al.* 2004), and supported by rich empirical evidence for organic matter processing in fresh waters (Boyero *et al.* 2011; Yvon-Durocher *et al.* 2012).

The decomposition model developed here extended the original exponential model formulated by Olson (1963) by

relaxing the assumption of constant decay rate, as proposed by Rovira & Rovira (2010). The general form of our model was

$$\frac{dX}{dt} = f(T)X \quad (5)$$

where X is the proportion of litter mass remaining at time t and $f(T)$ is a temperature-dependent function of decomposition rate. Following MTE, we expressed $f(T)$ as the Arrhenius equation:

$$f(T) = k_0 e^{\frac{-E}{T \cdot k_B}} \quad (6)$$

where k_0 is a normalisation constant, E is the apparent activation energy representing temperature sensitivity of litter decomposition rate, k_B is the Boltzmann constant (8.62×10^{-5} eV K⁻¹) and T is the absolute temperature in Kelvin. E in our model was estimated for each lake and leaf pack type as the negative slope of the linearised form of the Arrhenius equation (Brown *et al.* 2004). To test for a possible effect of crayfish invasion on the temperature sensitivity of litter decomposition rate, we used a multilevel linear regression approach, defining the intercept and slope (i.e. activation energy) of the linearised Arrhenius equation as a linear function of crayfish biomass (Supporting Information, SI 5).

The model of litter decomposition described above was then used to reconstruct seasonal patterns of leaf litter standing stock in lakes with increasing crayfish invasion intensity within the observed range (0–600 g trap⁻¹ night⁻¹). Predictions were made on a daily basis using a year-round time series of lake temperature derived from a continuous record of water temperature in seven of the study lakes in 2013–2014 (Fig. S1). Leaf litter standing stock was set to 100% on day zero of the model when litter input occurred. To evaluate the effect of crayfish invasion on detritus phenology, the time at which leaf litter standing stock was reduced to 20% was estimated from model simulations of litter decomposition with and without crayfish (modelled as decomposition of unconfined leaf packs and leaf packs confined in coarse mesh bags respectively). The time gap between the two conditions represented the magnitude of crayfish-induced shift in detritus phenology.

Independent of temperature, a change of litter quality through time, such as increasing concentration of refractory compounds, might have an additional effect on seasonal litter decomposition rates. This effect would, however, primarily become relevant at later stages of litter decomposition. In the interpretation of our model, we focused on the period where at least 20% of litter would still be remaining and thus assumed a very limited possible error due to change in litter quality.

The model of litter decomposition was fitted within a Bayesian framework and the shift in leaf detritus phenology was predicted from posterior values of model parameters (Supporting Information, SI 5). The joint posterior distributions of model parameters were obtained by means of MCMC sampling as implemented in the JAGS software in R using the package *rjags* (Plummer 2003). We ran three parallel MCMC chains and retained 25 000 iterations after an initial burn-in of 5000 iterations. Convergence of MCMC sampling was assessed using Brooks–Gelman–Rubin diagnostics (Brooks &

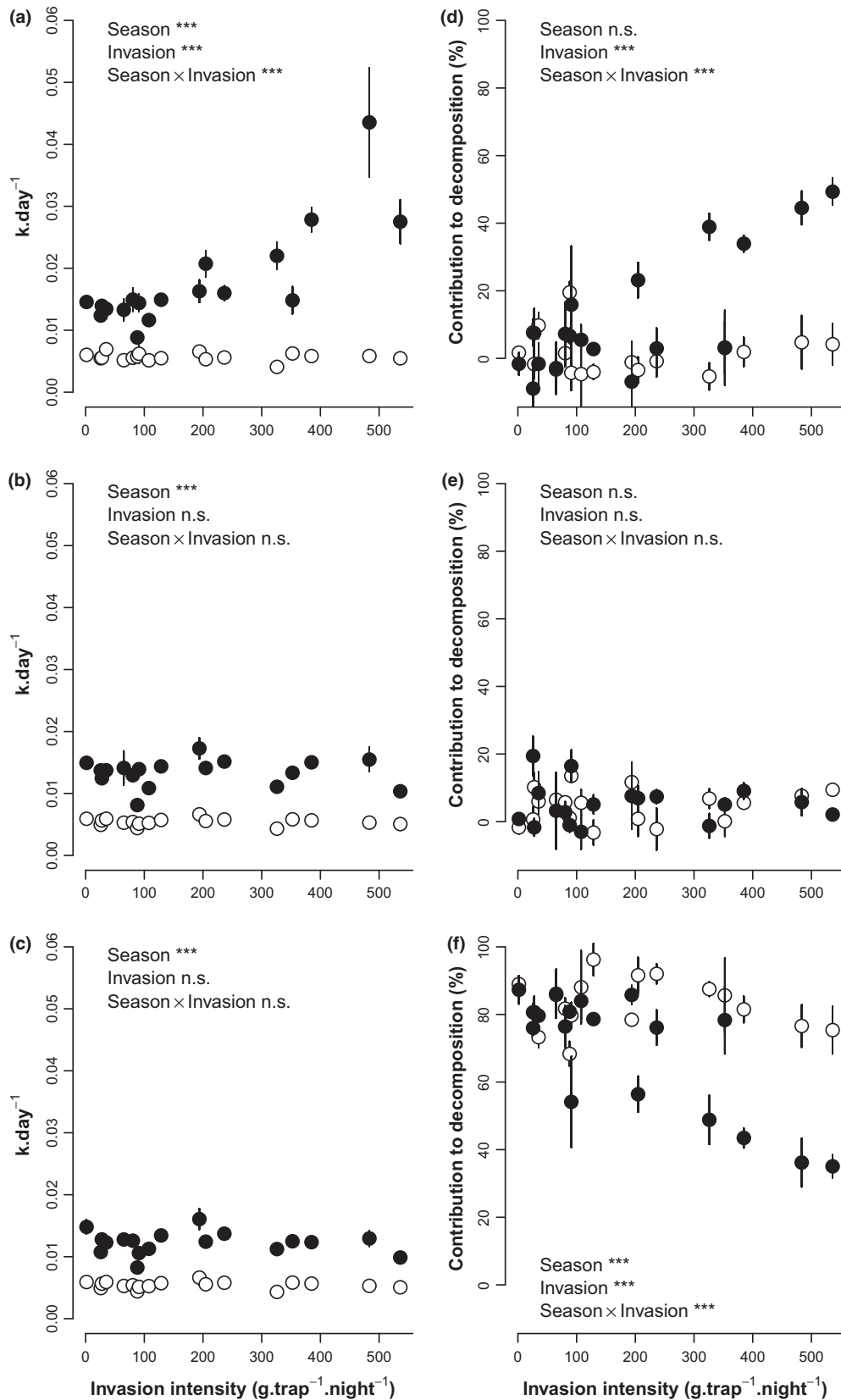


Figure 1 Litter decomposition rates and estimated contribution of different actors to decomposition in winter (white circles) and spring (black circles) 2014. Decomposition rates in unconfined leaf packs (a), confined leaf packs in coarse mesh bags (b) and fine mesh bags (c), and estimated contribution of crayfish (d), invertebrate detritivores (e) and microbial decomposers (f) to total decomposition. Error bars correspond to standard errors based on four independent data points per lake. Asterisks show the significance of single effects and their interaction as estimated with ANCOVA: *** $P < 0.001$, n.s. = not significant.

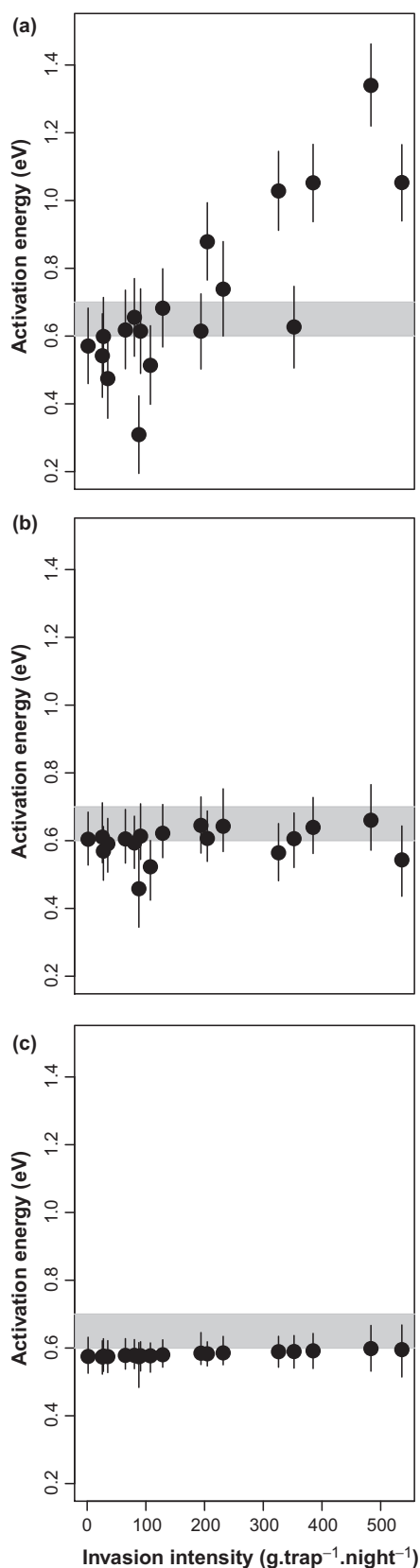


Figure 2 Variation in activation energy of leaf litter decomposition in relation to invasion intensity in the three leaf pack types. Posterior distributions of the activation energies (slopes noted as β ; Supporting Information, SI 5) are shown for unconfined leaf packs (a), and confined leaf packs in coarse mesh (b) and in fine mesh (c) bags across the observed range of invasion intensity. The median (black dots) and the 95% credible interval (error bars) are displayed. The grey zone corresponds to the range of metabolic theory of ecology predictions for activation energy of metabolic processes ($E = [0.6; 0.7]$ eV; Brown *et al.* 2004).

and explained variances (Gelman & Hill 2006). The percentage of either negative or positive values included into the posterior distribution was estimated to assess the probability of model parameters differing from zero.

RESULTS

In all leaf pack types across all lakes, litter decomposition rates were significantly higher in spring than in winter ($F_{1,32} > 318$, $P < 0.0001$; Fig. 1a–c; Table S7). The magnitude of this seasonal change in total decomposition rate (assessed by means of unconfined leaf packs) increased dramatically along the gradient of crayfish invasion intensity, as reflected by the significant interaction between Season and Invasion intensity ($F_{1,32} = 29.7$, $P < 0.0001$). In contrast, decomposition rates of leaf litter confined in both coarse and fine mesh bags were remarkably similar across all lakes and independent of the gradient of crayfish invasion intensity ($F_{1,32} < 0.5$, $P > 0.5$) in both seasons (Fig. 1b and c; Tables S5 and S7).

Crayfish invasion resulted in a change of the relative importance of actors involved in the process: litter decomposition shifted from predominantly microbial (on average 80% in all lakes in winter and less-invaded ones in spring; Fig. 1f) to being dominated by crayfish (up to 50% in highly invaded lakes in spring; Fig. 1d). Activity of other invertebrate detritivores accounted for a consistently small fraction of litter mass loss (4.9% on average) across lakes and seasons (Fig. 1e) and showed no relationship with crayfish density ($F_{1,32} = 0.4$, $P = 0.5$; Supporting Information, SI 4). This result reflected the low density and diversity of leaf-consuming invertebrates (predominantly asellids) found in all but one lake and independent of crayfish density across all lakes (Pearson correlation $r < 0.2$; $P > 0.6$; Supporting Information, SI 6). Thus, all collected evidence suggested that crayfish affected total decomposition rates by direct consumption of leaf litter.

Estimated by means of the Arrhenius model, the activation energy of decomposition (i.e. the negative slope of its relationship with temperature) ranged between 0.33 and 1.3 eV for total decomposition with crayfish (Fig. 2), and showed a steady increase along the gradient of invasion (Fig. 2a). In contrast, activity energy estimates for non-crayfish mediated decomposition remained similar and independent of crayfish biomass, being 0.58 eV [median; 95% CI: 0.49–0.66] for coarse mesh and 0.57 eV [median; 95% CI: 0.52–0.62] for fine mesh bags (Fig. 2b and c).

Predictions of our model for the seasonal dynamics of confined and unconfined leaf litter converged when zero crayfish biomass in lakes was assumed (Fig. 3a). In contrast, when high invasion intensity (600 g trap⁻¹ night⁻¹) was modelled, a

Gelman 1998). Uncertainties in model parameters and posterior predictions were reported using credible intervals (CI). Model fit was evaluated using posterior predictive P -values

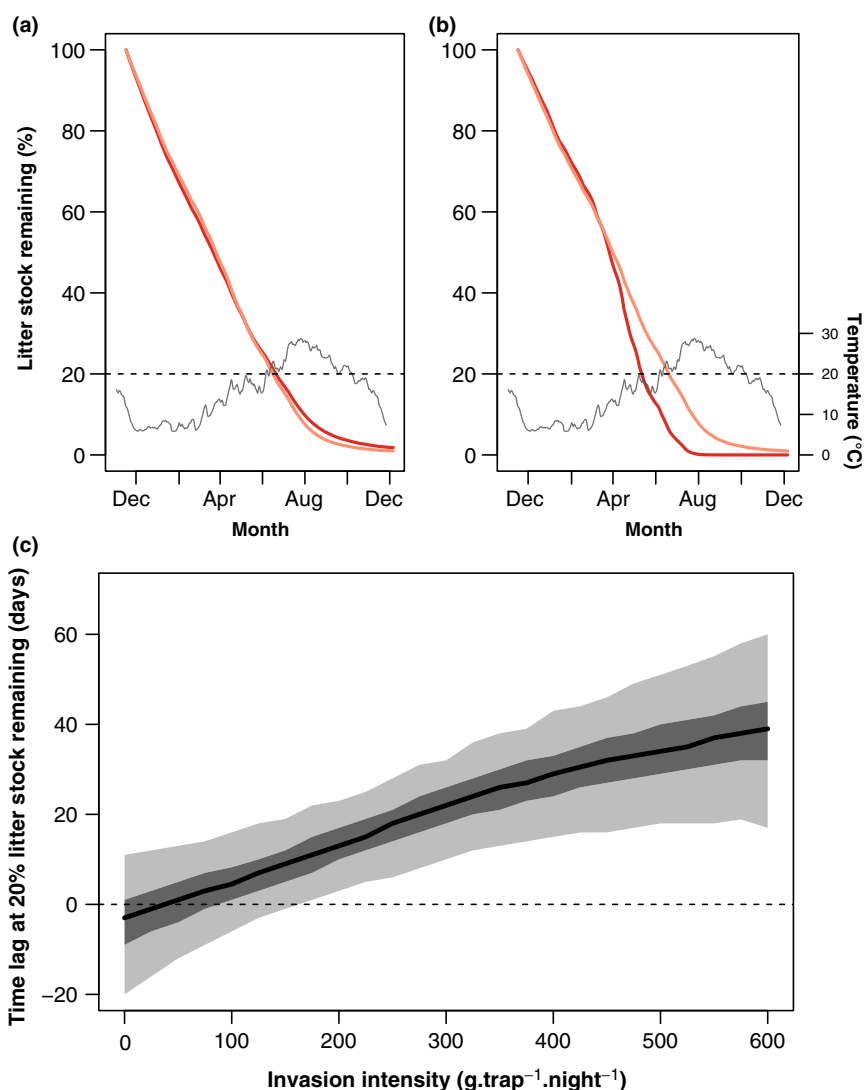


Figure 3 Consequences of crayfish invasion for leaf detritus phenology. Predicted seasonal loss of leaf stock as assessed in unconfined (red line) and confined (coarse mesh; orange line) leaf packs is shown at (a) no invasion (crayfish biomass: $0 \text{ g trap}^{-1} \text{ night}^{-1}$) and (b) high invasion intensity (crayfish biomass: $600 \text{ g trap}^{-1} \text{ night}^{-1}$). Predicted curves (medians) were drawn based on parameter values from randomly chosen 1000 MCMC samples. Mean daily water temperatures used in the model are also reported (grey line). (c) Predicted shift in the timing of litter stock depletion determined as the difference between unconfined leaf packs and leaf packs confined in coarse mesh bags. The median (black line) and the 95% (light grey area) and 50% (dark grey area) credible intervals based on randomly chosen 1000 MCMC subsamples are displayed.

crayfish effect on detritus standing stock became apparent in early spring (April, when 50% of litter standing stock was still remaining; Fig. 3b). Thus depletion of litter accessible to crayfish (unconfined leaf packs) was accelerated compared to the case of crayfish exclusion from the process (confined leaf packs). According to our model, while 2% of leaf litter stock would be remaining at the end of the yearly cycle in the absence of crayfish, nearly complete depletion of the stock would be reached in highly invaded ecosystems already in mid-July (Fig. 3b). This result corresponded to a strong shift in the timing of litter depletion: the mismatch (time lag) between the predictions of the model for decomposition in the presence and absence of crayfish for the date when 20% leaf litter standing stock would be remaining increased along the gradient of invasion intensity reaching up to 39 days (95% CI: 15–61 days; Fig. 3c).

DISCUSSION

While much attention has recently been given to the effects of climate warming on the timing of biological events, this study delivers unprecedented evidence that biological invasions also can have pronounced phenological consequences on freshwater ecosystems; here demonstrated through extending the concept of phenology to non-living stage of organisms and taking an ecosystem perspective. Using a gradient of crayfish invasion occurring across 18 lakes, we showed that, where non-native crayfish were abundant, they strongly accelerated leaf litter decomposition rates, taking over a dominant functional role in this major ecosystem process in spring and causing a substantial shift in seasonal resource patterns. Such biomass-driven phenological shifts are likely to be specific to biological invasions since invasive crayfish reach consistently higher den-

sities than native crayfish that could also be involved in litter decomposition (Hansen *et al.* 2013).

Ecological consequences of the phenological changes we show here may be very far-reaching and extend across levels of biological organisation and even across ecosystems. Importantly, invasive crayfish simultaneously affected both the form (ontogeny) and the temporal dynamics (phenology) of allochthonous carbon release into the ecosystem. In lakes without invasive crayfish, detrital carbon in the form of submerged leaf litter appears to follow a primarily microbial pathway and thus is converted into microbial biomass, dissolved organic matter and gases (Gessner *et al.* 1999). In the presence of invasive crayfish, an important part of detrital carbon is channelled more directly to secondary production of metazoans such as the crayfish themselves, their predators, and animals feeding on their faeces (Montemarano *et al.* 2007), thus bypassing the microbial pathway.

The acceleration of detritus decomposition by crayfish occurring in a specific period of time also induces a modification of the nature of detritus-derived resource input to food webs, shifting from slow continuous delivery (when detritus is processed by microbes) to an increasingly pulsed delivery. By affecting specific consumers directly, resource pulses often also result in indirect effects at the community level (Yang *et al.* 2008). For instance nutrients derived from leaf litter have been shown to play an important role in regulating spring dynamics of planktonic food webs in lakes (Fey *et al.* 2015). More pulsed delivery of detritus-derived nutrients through crayfish excretion has thus a high potential to either boost or suppress algal growth (depending on the matching of the spring time window of crayfish activity and algal growth) and to propagate through bottom-up effects to higher level consumers in pelagic food webs. Similarly, top-down effects could occur and even cross ecosystem borders as crayfish can subsidise numerous terrestrial and aquatic predators (Correia 2001; Bašić *et al.* 2015). On the long term, this could create novel temporal niche opportunities for some secondary consumers and result in persistent changes in community structure at different trophic levels (Yang *et al.* 2008) and modification of pathways of energy flows between different food web compartments, the latter enhanced by the mobility of crayfish (Ruokonen *et al.* 2013). In line with the recent call for introducing a temporal perspective into the studies of ecosystem ecology (McMeans *et al.* 2015), we emphasise the importance of validating these predictions on phenological shifts in nutrient fluxes and effects on temporal food web structure with further field observations and controlled experiments.

Another important implication of our findings is related to the role of invasive crayfish for the temperature sensitivity of litter decomposition. The seasonal model of litter decomposition used here was based on the theoretical principles of metabolic theory of ecology. Following MTE, apparent activation energy of any process driven by aerobic metabolism is predicted to conform to the theoretical range of values between 0.6 and 0.7 eV (Gillooly *et al.* 2001; Brown *et al.* 2004). While our estimates of apparent activation energy for non-crayfish leaf decomposition compare well with both theoretical predictions and previous empirical estimates for microbial litter

decomposition in fresh waters (0.58 eV; Boyero *et al.* 2011), the estimates for total decomposition involving crayfish displayed strong variability and were correlated with the gradient of invasion. Specifically, we found an enhanced temperature dependence of the process in lakes with high level of invasion (activation energy of up to 1.3 eV). Such systematic deviations from the predictions of the MTE have already been reported previously (Dell *et al.* 2011) and an increasing body of evidence suggests caution when assuming universality of the MTE predictions (Glazier 2015). Notably, in a study of latitude-driven temperature-dependence of decomposition, Boyero *et al.* (2011) found that the activation energy for invertebrate-driven decomposition was at odds with theory, concluding that an interplay of temperature and invertebrate occurrence and density determined the observed patterns in total litter decomposition. Here, a similar importance of the invader shredder density was demonstrated for the seasonal temperature dependence of litter decomposition. This is an alarming result, as it suggests a possibility of interaction between the functional effects of invasive species and climate warming.

Our study demonstrates that some powerful novel drivers of phenology other than climate warming appear to have been largely overlooked. The estimates of phenological shifts that we report attain several weeks and are stunning when considering that a single decade may be sufficient for many mobile invasive species to reach high densities and produce such effects (e.g. Wilson *et al.* 2004). In comparison, the average shifts in spring events such as the date of first flowering and leaf unfolding, butterfly emergence and bird migration reported to be driven by climate warming are estimated to be between 2.3 and 5.1 days per decade (Walther *et al.* 2002; Root *et al.* 2003). We show that an invasive species can have an effect on the phenology of an ecosystem process about an order of magnitude stronger than climate-induced shifts reported for the phenology of living organisms. Further investigations are clearly needed for understanding how phenological effects of invasive species might interact with those of globally rising temperatures.

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AUTHOR CONTRIBUTIONS

MA, JC and AL designed the research and performed the field and laboratory work. MB developed and implemented the Bayesian models. All authors contributed to data analysis. MA wrote the first draft and all authors contributed substantially to revisions.

REFERENCES

- Bašić, T., Britton, J.R., Jackson, M., Reading, P. & Grey, J. (2015). Angling baits and invasive crayfish as important trophic subsidies for a large cyprinid fish. *Aquat. Sci.*, *77*, 153–160.
- Boyero, L., Pearson, R.G., Gessner, M.O., Barmuta, L.A., Ferreira, V., Graça, M.A.S. *et al.* (2011). A global experiment suggests climate warming will not accelerate litter decomposition in streams but might reduce carbon sequestration. *Ecol. Lett.*, *14*, 289–294.
- Brooks, S.P. & Gelman, A. (1998). General methods for monitoring convergence of iterative simulations. *J. Comput. Graph. Stat.*, *7*, 434–455.
- Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M. & West, G.B. (2004). Toward a metabolic theory of ecology. *Ecology*, *85*, 1771–1789.
- Cleland, E.E., Chuine, I., Menzel, A., Mooney, H.A. & Schwartz, M.D. (2007). Shifting plant phenology in response to global change. *Trends Ecol. Evol.*, *22*, 357–365.
- Collas, M., Julien, C. & Monnier, D. (2007). Note technique : La situation des écrevisses en France. Résultats des enquêtes nationales réalisées entre 1977 et 2006 par le conseil supérieur de la pêche. *Bull. Fr. Pêche Piscic.* *386*, 1–39.
- Correia, A.M. (2001). Seasonal and interspecific evaluation of predation by mammals and birds on the introduced red swamp crayfish *Procambarus clarkii* (Crustacea, Cambaridae) in a freshwater marsh (Portugal). *J. Zool. (Lond.)*, *255*, 533–541.
- Croll, S.L. & Watts, S.A. (2004). The effect of temperature on feed consumption and nutrient absorption in *Procambarus clarkii* and *Procambarus zonangulus*. *J. World Aquac. Soc.*, *35*, 478–488.
- Cummins, K.W., Wilzbach, M.A., Gates, D.M., Perry, J.B. & Taliaferro, W.B. (1989). Shredders and riparian vegetation. *Bioscience*, *39*, 24–30.
- Dell, A.I., Pawar, S. & Savage, V.M. (2011). Systematic variation in the temperature dependence of physiological and ecological traits. *Proc. Natl Acad. Sci. USA*, *108*, 10591–10596.
- Dunoyer, L., Dijoux, L., Bollache, L. & Lagrue, C. (2014). Effects of crayfish on leaf litter breakdown and shredder prey: are native and introduced species functionally redundant? *Biol. Invas.*, *16*, 1545–1555.
- Edwards, M. & Richardson, A.J. (2004). Impact of climate change on marine pelagic phenology and trophic mismatch. *Nature*, *430*, 881–884.
- Espina, S., Diaz Herrera, F. & Bueckle, R.L.F. (1993). Preferred and avoided temperatures in the crawfish *Procambarus clarkii* (Decapoda, Cambaridae). *J. Therm. Biol.*, *18*, 35–39.
- Fey, S.B., Mertens, A.N. & Cottingham, K.L. (2015). Autumn leaf subsidies influence spring dynamics of freshwater plankton communities. *Oecologia*, *178*, 875–885.
- Gelman, A. & Hill, J. (2006). *Data Analysis Using Regression and Multilevel Hierarchical Models*. Cambridge University Press, New York.
- Gessner, M.O., Chauvet, E. & Dobson, M. (1999). A perspective on leaf litter breakdown in streams. *Oikos*, *85*, 377–384.
- Gillooly, J.F., Brown, J.H., West, G.B., Savage, V.M. & Charnov, E.L. (2001). Effects of size and temperature on metabolic rate. *Science*, *293*, 2248–2251.
- Glazier, D.S. (2015). Is metabolic rate a universal ‘pacemaker’ for biological processes? *Biol. Rev. Camb. Philos. Soc.*, *90*, 377–407.
- Gutierrez-Yurrita, P.J., Sancho, G., Bravo, M.A., Baltanas, A. & Montes, C. (1998). Diet of the red swamp crayfish *Procambarus clarkii* in natural ecosystems of the Doñana National Park temporary fresh-water marsh (Spain). *J. Crust. Biol.*, *18*, 120–127.
- Handa, I.T., Aerts, R., Berendse, F., Berg, M.P., Bruder, A., Butenschoen, O. *et al.* (2014). Consequences of biodiversity loss for litter decomposition across biomes. *Nature*, *509*, 218–221.
- Hansen, G.J.A., Vander Zanden, M.J., Blum, M.J., Clayton, M.K., Hain, E.F., Hauxwell, J. *et al.* (2013). Commonly rare and rarely common: comparing population abundance of invasive and native aquatic species. *PLoS ONE*, *8*, e77415.
- Hobbs, H.H., Jass, J.P. & Huner, J.V. (1989). A review of global crayfish introductions with particular emphasis on two North American species (Decapoda, Cambaridae). *Crustaceana*, *56*, 299–316.
- Lecerf, A., Dobson, M., Dang, C. & Chauvet, E. (2005). Riparian plant species loss alters trophic dynamics in detritus-based stream ecosystems. *Oecologia*, *146*, 432–442.
- McMeans, B.C., McCann, K.S., Humphries, M., Rooney, N. & Fisk, A.T. (2015). Food web structure in temporally-forced ecosystems. *Trends Ecol. Evol.*, *30*, 662–672.
- Montemarano, J.J., Kershner, M.W. & Leff, L.G. (2007). Crayfish effects on fine particulate organic matter quality and quantity. *Fund. Appl. Limnol.*, *169*, 223–229.
- Moore, J.C., Berlow, E.L., Coleman, D.C., de Ruiter, P.C., Dong, Q., Hastings, A. *et al.* (2004). Detritus, trophic dynamics and biodiversity. *Ecol. Lett.*, *7*, 584–600.
- Noormets, A. (2009). *Phenology of Ecosystem Processes*. Springer, Dordrecht.
- Odling-Smee, F.J., Laland, K.N. & Feldman, M.W. (2003). *Niche Construction: The Neglected Process in Evolution*. Princeton University Press, Princeton.
- Olson, J.S. (1963). Energy storage and the balance of producers and decomposers in ecological systems. *Ecology*, *44*, 322–331.
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. & R Core Team (2015). nlme: linear and nonlinear mixed effects models. *R package version*, *3*. 1–117.
- Plummer, M. (2003). JAGS: a program for analysis of Bayesian graphical models using Gibbs sampling. *Proc. Inter. Workshop Distri. Statist. Comput.*, *124*, 125.
- R Core Team (2013). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available at: <http://www.R-project.org/>. Last accessed 1 December 2015.
- Rodríguez, C., Bécares, E. & Fernandez-Alaez, M. (2003). Shift from clear to turbid phase in Lake Chozas (NW Spain) due to the introduction of American red swamp crayfish (*Procambarus clarkii*). *Hydrobiologia*, *506*–509, 421–426.
- Rooney, N. & McCann, K.S. (2012). Integrating food web diversity, structure and stability. *Trends Ecol. Evol.*, *27*, 40–46.
- Root, T.L., Price, J.T., Hall, K.R., Schneider, S.H., Rosenzweig, C. & Pounds, J.A. (2003). Fingerprints of global warming on wild animals and plants. *Nature*, *421*, 57–60.
- Rovira, P. & Rovira, R. (2010). Fitting litter decomposition datasets to mathematical curves: towards a generalised exponential approach. *Geoderma*, *155*, 329–343.
- Ruokonen, T.J., Kiljunen, M., Karjalainen, J. & Hamalainen, H. (2013). Invasive crayfish increase habitat connectivity: a case study in a large boreal lake. *Knowl. Manag. Aquat. Ecosyst.*, *407*, 08.
- Schwartz, M. (2003). *Phenology: An Integrative Environmental Science*. Kluwer Academic Publishers, Dordrecht.
- Simberloff, D., Martin, J.-L., Genovesi, P., Maris, V., Wardle, D.A., Aronson, J. *et al.* (2013). Impacts of biological invasions: what’s what and the way forward. *Trends Ecol. Evol.*, *28*, 58–66.
- Stachowicz, J.J. & Tilman, D. (2005). Species invasions and the relationships between species diversity, community saturation, and ecosystem functioning. In: *Species Invasions: Insights, Into Ecology, Evolution and Biogeography* (eds Sax, D.F., Stachowicz, J.J. & Gaines, S.D.). Sinauer, Sunderland, MA, pp. 41–64.
- Strayer, D.L. (2010). Alien species in fresh waters: ecological effects, interactions with other stressors, and prospects for the future. *Freshw. Biol.*, *55*, 152–174.
- Thackeray, S.J., Sparks, T.H., Frederiksen, M., Burthe, S., Bacon, P.J., Bell, J.R. *et al.* (2010). Trophic level asynchrony in rates of phenological change for marine, freshwater and terrestrial environments. *Glob. Chang. Biol.*, *16*, 3304–3313.
- Twardochleb, L.A., Olden, J.D. & Larson, E.R. (2013). A global meta-analysis of the ecological impacts of nonnative crayfish. *Freshw. Sci.*, *32*, 1367–1382.
- Usio, N. (2000). Effects of crayfish on leaf processing and invertebrate colonisation of leaves in a headwater stream: decoupling of a trophic cascade. *Oecologia*, *124*, 608–614.
- Vojtkovska, R., Horka, I. & Duris, Z. (2014). The diet of the spiny-cheek crayfish *Orconectes limosus* in the Czech Republic. *Centr. Eur. J. Biol.*, *9*, 58–69.
- Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesani, C., Beebee, T.J.C. *et al.* (2002). Ecological responses to recent climate change. *Nature*, *416*, 389–395.

- Wilson, K.A., Magnuson, J.J., Lodge, D.M., Hill, A.M., Kratz, T.K., Perry, W.L. *et al.* (2004). A long-term rusty crayfish (*Orconectes rusticus*) invasion: dispersal patterns and community change in a north temperate lake. *Can. J. Fish Aquat. Sci.*, 61, 2255–2266.
- Winder, M. & Schindler, D.E. (2004). Climate change uncouples trophic interactions in an aquatic ecosystem. *Ecology*, 85, 2100–2106.
- Wolkovich, E.M. & Cleland, E.E. (2010). The phenology of plant invasions: a community ecology perspective. *Front. Ecol. Environ.*, 9, 287–294.
- Yang, L.H., Bastow, J.L., Spence, K.O. & Wright, A.N. (2008). What can we learn from resource pulses? *Ecology*, 89, 621–634.
- Yvon-Durocher, G., Caffrey, J.M., Cescatti, A., Dossena, M., Giorgio, P.D., Gasol, J.M. *et al.* (2012). Reconciling the temperature dependence of respiration across timescales and ecosystem types. *Nature*, 487, 472–476.

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