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Impact of an invasive alien plant on litter decomposition along a latitudinal gradient

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Abstract. Invasive alien plant effects on ecosystem functions are often difficult to predict across environmental gradients due to the context-dependent interactions between the invader and the recipient communities. Adopting a functional trait-based framework could provide more mechanistic predictions for invasive species' impacts. In this study, we contrast litter decomposition rates among communities with and without the invasive plant *Impatiens glandulifera* in five regions along a 1600 km long latitudinal gradient in Europe. Across this gradient, four functional traits, namely leaf dry matter content (LDMC), specific leaf area (SLA), stem-specific density (SSD), and plant height, are correlated to rates of litter decomposition of standardized rooibos (labile), green tea (recalcitrant), and *I. glandulifera* litter. Our results show that both invaded and non-invaded plant communities had a higher expression of acquisitive traits (low LDMC and SSD, high SLA) with increasing temperature along the latitudinal gradient, partly explaining the variation in decomposition rates along the gradient. At the same time, invasion shifted community trait composition toward more acquisitive traits across the latitudinal gradient. These trait changes partly explained the increased litter decomposition rates of the labile litter fraction of rooibos and *I. glandulifera* litter in invaded communities, a shift that was most evident in the warmer study regions. Plant available nitrogen was lower in invaded communities, likely due to high nutrient uptake by *I. glandulifera*. Meanwhile, the coldest study region was characterized by a reversed effect of invasion on decomposition rates. Here, community traits related to low litter quality and potential allelopathic effects of the invader resulted in reduced litter decomposition rates, suggesting a threshold temperature at which invader effects on litter decomposition turn positive. This study therefore illustrates how functional trait changes toward acquisitive traits can help explain invader-induced changes in ecosystem functions such as increased litter decomposition.

Key words: ecosystem function; functional traits; *Impatiens glandulifera;* invasive alien species; latitudinal gradient; leaf dry matter content; litter decomposition; plant available nitrogen; specific leaf area; stem-specific density; tea bag index.

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INTRODUCTION

In an increasingly globalized world, the number of alien plant species invading plant communities continues to rise (van Kleunen et al. 2015). One major concern is that invasive alien species will lead to significant changes in functioning of the invaded ecosystem (e.g., Dassonville et al. 2008, Pyšek et al. 2012). Litter decomposition is one of these ecosystem functions which is potentially strongly affected by invasive alien plants (Ehrenfeld 2003, Aerts et al. 2017). A recent global meta-analysis across 94 studies (Liao et al. 2008) revealed an increase in litter decomposition rates of approximately 117% in invaded communities. However, the impact of invasive alien plants on litter decomposition is not consistent, with several studies finding no change or even a decrease in decomposition rates (Ehrenfeld 2003, Liao et al. 2008, Broadbent et al. 2017). This context-dependency of the invasive alien plants' effects is expected to be, at least partly, governed by the interaction between the functional (leaf) traits of the invading non-native and the recipient communities, respectively (Suding et al. 2008). Thus, adopting a functional trait-based approach could provide a more mechanistic predictive framework for studying invasive alien species' impact on ecosystem functioning (Suding et al. 2008, Finerty et al. 2016; K. Helsen, *unpublished manuscript*).

Several functional leaf traits have been demonstrated to affect litter quality and thus leaf litter decomposition rates at the species level (Cornelissen et al. 1999, Cornwell et al. 2008, Freschet et al. 2012*a*). More specifically, leaf traits associated with fast growth and resource acquisition, such as high leaf nutrient concentrations, high specific leaf area (SLA), low leaf dry matter content (LDMC) as well as leaf toughness and thickness, have been shown to directly relate to faster leaf litter decomposition rates (Allison and Vitousek 2004, Wright et al. 2004, Kazakou et al. 2006, Orwin et al. 2010). Similarly, stem traits such as low stem-specific density (SSD) also (indirectly) relate to fast leaf litter decomposition (Szefer et al. 2017). The species-level link between leaf traits and litter decomposition has also been shown to translate to the community level, with community-weighted mean (CWM) traits relating to decomposition rates of the community litter (Garnier et al. 2004, Quested et al. 2007, Finerty et al. 2016, García-Palacios et al. 2017).

The effects of functional traits on litter decomposition do not exclusively relate to litter quality (Dias et al. 2017). Several studies have shown significant correlations between community trait composition and litter decomposition using standard litter (Scherer-Lorenzen 2008, McLaren and Turkington 2011, Yahdjian et al. 2017), suggesting positive effects of acquisitive plant traits on the decomposition environment and/or decomposer communities (Hector et al. 2000, McLaren and Turkington 2011, Freschet et al. 2012*b*). The prevalence of strong links between plant identity (and trait composition) and the decomposer community is further supported by the frequently observed home field advantage, where a species' litter tends to decompose fastest in its own soil (Veen et al. 2015). Moreover, community-level functional plant traits have been shown to affect the decomposer community composition, with a shift to bacterial-dominated microbial communities and associated higher rates of decomposition and nutrient turnover under communities with acquisitive plant traits (Orwin et al. 2010, de Vries et al. 2012).

Invasive alien plants can potentially affect the invaded plant community's functional trait set (CWM), and thus litter decomposition rate, in two non-exclusive ways. First, the invasive alien plant can introduce novel trait values to the invaded community, consequently shifting the overall trait composition of the community merely through its presence (Finerty et al. 2016). Many invasive alien plants are highly competitive species characterized by fast growth and resource acquisition (Wright et al. 2004, van Kleunen et al. 2010), which are in turn associated with functional leaf traits that are known to result in more decomposable litter (Allison and Vitousek 2004, Kazakou et al. 2006, Orwin et al. 2010). Secondly, invaders can alter the community-level trait set either by competition-driven changes in the invaded community's species composition (Hejda and de Bello 2013) or by changes in its trait composition due to intraspecific trait changes (K. Helsen, *unpublished manuscript*).

At increasing spatial extent, the greatest determinant of variation in litter decomposition is variation in the physiochemical environment, that is, climate and soil conditions (Hättenschwiler et al. 2005, García-Palacios et al. 2016). This variation may affect the impact of invasive alien species on litter decomposition (Ehrenfeld 2003). Furthermore, most successful invaders are characterized by a very high potential for phenotypic (trait) plasticity across their (invaded) range (Davidson et al. 2011). The expected increased relative importance of competition compared to other interactions under environmentally favorable conditions (cf. the stress gradient hypothesis, Bertness and Callaway 1994) could result in shifts toward more acquisitive (leaf) traits in the invasive alien plant and thus a greater increase in the litter decomposition rate of invaded communities in parts of its invaded range. Since most invasive alien species occur along relatively large environmental gradients, there is a need for large-scale studies to adequately understand invader effects on community-level trait values and ecosystem functioning along these gradients (Kramer et al. 2012, Stotz et al. 2017).

Despite some early successful explorations of a functional trait-based framework on the effects of invasive alien species on ecosystem functioning (Scharfy et al. 2011, Castro-Díez et al. 2016; K. Helsen, *unpublished manuscript*), no study, to our knowledge, has investigated this framework for litter decomposition, nor have studies explored effects along a wide environmental gradient. Here, we address this knowledge gap by using the invasive alien plant *Impatiens glandulifera* Royle as a study species. This species is known to exhibit high trait variation along its invaded range in Europe (Kollmann and Bañuelos 2004, Acharya 2014). In this study, we compared several litter decomposition measures between invaded and non-invaded plant communities for a total of 25 populations spread across five regions along a 1600 km long latitudinal gradient, from Belgium (51.0° N) to central Norway (63.5° N). By using standardized litter (including litter of the invasive species), we excluded the direct effects of litter quality on decomposition rates, allowing us to evaluate indirect effects of community trait composition on litter decomposition rates. Using four functional traits (LDMC, SLA, SSD, and plant height) for both *I. glandulifera* and the local plant communities across the studied latitudinal gradient, we answered the following research questions:

1. Does invasion by *I. glandulifera* induce community-level functional trait changes?
2. Does invasion by *I. glandulifera* affect rates of standard litter decomposition and plant available nitrogen, independent of effects on litter quality?
3. Is variation in litter decomposition associated with changes in the functional trait composition of the invaded communities?
4. Do *I. glandulifera* invasion-induced effects on standard litter decomposition become stronger toward the southern end of the latitudinal gradient due to increasingly more favorable (i.e., warmer and/or wetter) conditions?

METHODS

Study species

Impatiens glandulifera Royle (Balsaminaceae) was originally introduced in Europe as an ornamental plant in the 1800s from the western Himalaya (Beerling and Perrins 1993). The species subsequently became invasive, rapidly colonizing riparian habitats across its invaded range from southern Spain (37° N) to northern Norway (70° N). *Impatiens glandulifera* is a large, competitive annual plant of up to 2.5 m high and produces a large number of transient seeds. Seeds are dispersed through both ballistochory and hydrochory along waterways, partly explaining its invasion success (Beerling and Perrins 1993). The species produces naphthoquinones (a group of polycyclic aromatic hydrocarbons), which are released in the soil early in the growing season through leaching and have allelopathic properties (Ruckli et al. 2014).

Study design

We studied *I. glandulifera* populations in five regions along a 1600 km latitudinal gradient, ranging from Ghent, Belgium, in the south to Trondheim, Norway, in the north (Table 1). In each study region, five *I. glandulifera* populations were selected in open vegetation along wooded

Table 1. Locations and climate characteristics for the five study regions along the latitudinal gradient.

Study region	Nearest city	Lat (°N)	Lon (°E)	T_{BP} (°C)	P_{BP} (mm)	MAT (°C)	MAP (mm)	Burial date (Julian days)	Retrieval date (Julian days)
Belgium	Ghent	51.0	3.8	18.8	91	10.2	754	189–194	236–241
Northwest Germany	Bremen	53.1	8.8	18.2	30	8.8	732	200–205	244
South Sweden	Landskrona	55.9	12.8	17.1	74	8.0	642	209–215	255–257
Central Sweden	Stockholm	59.3	17.9	14.9	51	7.0	527	220–224	265–266
Central Norway	Trondheim	63.5	11.0	12.3	129	5.0	871	230–235	277

Notes: T_{BP}, average temperature during the burial period; P_{BP}, total precipitation during the burial period (burial date to retrieval date); MAT, mean annual temperature; MAP, mean annual precipitation; PRS, Plant Root Simulator. Tea bags and PRS probes were in situ from the burial date to the retrieval date.

edges and river banks, but not in fully shaded conditions, resulting in a total of 25 populations. During the summer of 2016, we established four 3 × 3 m plots at each selected population, two within patches containing *I. glandulifera* (*I. glandulifera* cover ≥65%), termed "invaded plots," and two in patches without *I. glandulifera* (*I. glandulifera* absent), termed "control plots," with a maximum distance of 20 m between invaded and controls plots. When establishing plots, care was taken to minimize variation in other biotic and abiotic conditions (slope, aspect, soil type, and distance to wooded edge).

Litter decomposition proxies

Litter decomposition was assessed using litterbags with standard litter types. More specifically, we used the tea bag index method and buried Lipton green tea and Lipton rooibos nylon-mesh tea bags in each plot (Keuskamp et al. 2013). The decomposition rate of green tea is much higher than that of the rooibos. Consequently, the labile fraction of the green tea is completely decomposed at the end of the burial period and is thus indicative of the amount of the initial labile litter fraction that becomes recalcitrant (the stabilization factor [S] of the exponential decay function; cf. Keuskamp et al. 2013). Rooibos, on the other hand, retains part of the initial labile fraction at the end of the burial period and is thus indicative of the initial decomposition rate of the labile fraction (rate constant k of the exponential decay function; cf. Keuskamp et al. 2013). We complemented this setup with four nylon-mesh litterbags (opened, filled, and resealed Lipton tea bags) filled with 1.250 g oven-dried *I. glandulifera* leaf material for each plot. *Impatiens glandulifera* leaf material was collected from a previous greenhouse study and consisted of a mixed leaf sample of 73 full grown *I. glandulifera* plants (K. Helsen, *unpublished manuscript*). *Impatiens glandulifera* leaf material consisted of small leaf fragments of 0.5–3 cm^2.

This setup resulted in four tea bag triplets per plot, each consisting of Lipton green tea, and Lipton rooibos and *I. glandulifera* leaf material, which were buried during the 2016 growing season in the four corners of each 3 × 3 m plot, at a distance of 1.2 m from the plot center (Table 1). Note that tea bags allow microorganisms and mesofauna to enter the bags, but exclude macrofauna (mesh size 0.25 mm; Keuskamp et al. 2013). Mass loss was assessed for each tea bag after approximately six weeks; although shorter than the advised 12 weeks, green tea decomposition of the labile litter is known to be completed after 40 d at 15°C (Keuskamp et al. 2013). After collection, litterbags were cleaned (dry brush) and oven-dried at 70°C for 48 h, using a precision balance (0.1 mg accuracy) and averaged for each plot for each litter type (green tea, rooibos, and *I. glandulifera* leaves). Approximately 85% of the litterbags were used for statistical analysis, due to exclusion of lost and damaged bags (i.e., holes).

Latitudinal effects: environmental variables

Variation along the latitudinal gradient was quantified using climatic and soil conditions, given their importance for the decomposition process. Average daily temperature (T_{BP}) and total precipitation (P_{BP}) were calculated for the exact burial period (in days) for each plot (Table 1), based on daily air temperature and precipitation data from meteorological weather stations. Weather data were obtained for the closest city to each study region from NOAA for Germany and Norway (NOAA 2017), from SMHI for the two study regions in Sweden

(SMHI 2017) and from the KMI weather station in Melle for Belgium (KMI 2017).

In parallel with the tea bag triplets, we established four pairs of PRS probes (Plant Root Simulator, Western Ag Innovations, Saskatoon, Canada) per plot, to assess soil nitrogen availability (NH^{4+} and NO^{3-}) over a time period of approximately six weeks during the growing season (Table 1). The four PRS probe pairs were inserted vertically into the soil, in locations perpendicular to the tea bags (1.2 m from the plot center) at the same time as tea bag burial. Most probes were retrieved for all but two plots from the south Swedish study region (96% retrieval rate). Probes were subsequently shipped to Western Ag Innovations to calorimetrically quantify NO^{3-} and NH^{4+} levels using an automated flow injection analysis system.

We additionally collected one soil sample (consisting of four random pooled subsamples) from the upper 8 cm of the soil in each plot. Soil samples were dried at 60°C and sieved using a 2-mm sieve. Soil pH was subsequently measured on a 1:1 soil/distilled water solution after 5 min stirring and 1 h resting, using a PHM82 standard pH meter (Radiometer A/S Copenhagen) for the collected soil samples of each plot location.

Community and functional trait measurements

Species abundance (% ground cover) of all vascular plants was estimated for each plot using fixed abundance groups (at 5% cover intervals). We subsequently measured four functional traits for each species (including *I. glandulifera*) with an abundance >10% at the plot level. These traits included LDMC, SLA, SSD, and plant height. The first three traits were selected because of their previously demonstrated link to litter decomposition rates (Allison and Vitousek 2004, Kazakou et al. 2006, Orwin et al. 2010). Plant height was included since it is typically part of another general trait variation axis independent of the leaf economics trait axes, but related to competitive ability (Wright et al. 2004, Díaz et al. 2016). Plant height was hence used to assess the effect of this independent trait axis on litter decomposition. Traits were measured for a minimum of 20 samples per plot, according to standardized protocols (Pérez-Harguindeguy et al. 2013). Leaf area was measured on fresh leaves within 48 h of collection using a Canoscan LiDe 120 flatbed scanner (Canon, Japan). Leaf fresh and dry weights (after 72-h oven-drying at 60°C) were assessed with a precision balance (0.1 mg accuracy). In total, we assessed functional traits for 453 species-plot combinations of 50 different species.

We calculated community abundance-weighted mean trait values for each of the four functional traits per plot. These CWM values were calculated twice, once including and once excluding *I. glandulifera* traits. To assess species composition, we performed a constrained correspondence analysis (CCA) ordination on the abundance-weighted plot × species matrix (excluding *I. glandulifera* presence) with the vegan R package (Oksanen et al. 2017). The ordination was constrained by latitude, longitude, T_{BP}, P_{BP}, and invasion status (control vs. invaded plot). We furthermore calculated the mean abundance-weighted functional competition signature (C-signature) and functional stress signature (S-signature) for each plot excluding *I. glandulifera*, based on the C-S-R plant functional type system of Grime (1977; Hunt et al. 2004). Species richness was defined as the total number of species present in each plot.

Data analysis

The potential invasion effect on community species compositions was tested with a permutation ANOVA (9999 permutations) on the invasion status constrain in the CCA ordination. Invasion effects on species richness and community composition were additionally assessed using linear mixed-effects models (LMMs) with invasion status (control vs. invaded plot) as a fixed factor. This model was performed separately for species richness, C-signature, and S-signature as response variables. We performed analogous LMMs on the CWM values (excluding *I. glandulifera* traits) for each measured functional traits (plant height, LDMC, SLA, SSD), including invasion status as a fixed factor and T_{BP}, P_{BP}, soil pH, C-signature, and S-signature as fixed covariates. First-order interaction terms between invasion status and all fixed covariates were also included. Similar LMM analyses were also performed for all measured traits for *I. glandulifera* (albeit without the invasion status factor). We also calculated the difference between the CWM trait value and the trait value of *I. glandulifera* for each invaded plot (community-invader trait difference). We then performed a simple intercept

LMM for each community-invader trait difference to assess whether trait differences were significantly different from zero.

Next, we performed several analogous LMMs for each measured litter decomposition proxy (% rooibos, % green tea, % *Impatiens* mass loss) and plant available N. These models included invasion status as a fixed factor and T_{BP}, P_{BP}, soil pH, C-signature, S-signature, and the CWM of all four measured functional traits as covariates. First-order interaction terms between invasion status and all covariates were also included. These models were run twice for each response variable, once with the CWM trait values including *I. glandulifera* traits and again excluding *I. glandulifera* traits. All LMMs were reduced using stepwise model reduction based on Akaike's information criteria (AIC) for the ML estimation models (cf. Zuur et al. 2009). This approach allowed us to evaluate the importance of including *I. glandulifera* traits in explaining litter decomposition variation among plots.

The random effect structure for all LMMs consisted of a random intercept term for population identity nested in study region. This random effect structure was selected based on AIC following the protocol of Zuur et al. (2009). All final LMM output was based on REML estimations, with standardized beta coefficients, with all LMMs performed with the nlme R package (Pinheiro et al. 2017). Semi-partial R^2_β coefficients were calculated for each covariate using the method of Edwards et al. (2008). Several response and predictor (covariates) variables were transformed to meet model assumptions, namely normal distribution and independence of residuals (Tables 2, 3). All predictors were checked for multicollinearity using variance inflation factors (conservative threshold of VIF = 5) before LMM analyses. Collinearity was observed for CWM LDMC and CWM SLA (VIF > 5). For this reason, models including CWM traits as predictors were run twice, once including only CWM LDMC and once including only CWM SLA, and AIC values were subsequently compared. Intercorrelations between the four measured traits and between the three litter decomposition proxies and available N were assessed with Pearson correlations. Variation in abiotic and biotic variables along the studied latitudinal gradient was assessed using Spearman rank correlations between T_{BP}, P_{BP}, soil pH, C-signature, S-signature, and latitude. All statistical analyses were performed in SPSS 21.0 (SPSS, Chicago, Illinois, USA) or R 3.3.3 (R Core Team 2017).

Table 2. Parameter estimates of the linear mixed-effects models on functional trait values.

	Plant height			LDMC†			SLA			SSD		
Parameters	β	*F*	R^2_β	β	*F*	R^2_β	β	*F*	R^2_β	β	*F*	R^2_β
CWM traits												
Invasion status	–	–	–	β_C 24.98 β_I 22.59	5.7*	0.075	β_C 2.86 β_I 5.96	9.6**	0.119	β_C 4.59 β_I 2.41	4.8*	0.064
T_{BP}	−2.10	4.4*	0.058	−2.74	7.5**	0.097	4.27	18.3***	0.204	−5.88	34.6***	0.330
C-signature	6.57	43.2***	0.372	5.44	29.6***	0.297	−3.28	10.8**	0.132	7.52	56.5***	0.447
S-signature‡	–	–	–	7.39	54.5***	0.438	−3.78	14.3***	0.168	8.31	69.1***	0.497
Invasion status*T_{BP}	–	–	–	β_C −2.74 β_I −0.76	3.9$^{(*)}$	0.053	–	–	–	β_C −5.88 β_I −4.07	3.3$^{(*)}$	0.045
Impatiens glandulifera traits												
T_{BP}	–	–	–	–	–	–	2.33	5.7*	0.192	−2.29	5.3*	0.180
P_{BP}	−2.07	4.3*	0.152	–	–	–	–	–	–	−1.55	2.7$^{(*)}$	0.101

Notes: C-signature, mean abundance-weighted functional competition signature; S-signature, mean abundance-weighted functional stress signature; T_{BP}, average temperature during the burial period; P_{BP}, total precipitation during the burial period; β_C, beta coefficient for control plots; β_I, beta coefficient for invaded plots. Results for both the community-weighted mean (CWM) trait and *I. glandulifera* trait models for each trait (i.e., plant height, leaf dry matter content [LDMC], specific leaf area [SLA], and stem-specific density [SSD]). Standardized beta coefficients, test statistics (*F*), and semi-partial R^2_β are given for each retained predictor after model reduction. N = 100 for CWM trait models, N = 50 for *I. glandulifera* trait models.

$^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$.

† Logarithm transformation.

‡ Square root transformation.

Table 3. Parameter estimates of the linear mixed-effects models on litter decomposition proxies and plant available nitrogen.

	% rooibos†			% green tea†			% *Impatiens*			Plant available N§		
Parameters	β	F	R^2_β	β	F	R^2_β	β	F	R^2_β	β	F	R^2_β
Invasion status	β_C 7.25 β_I 5.19	4.3*	0.060	–	–	–	β_C 14.56 β_I 16.78	4.9*	0.068	β_C 5.54 β_I 2.28	10.6**	0.132
T_{BP}	1.30	1.7	0.025	1.72	2.9$^{(*)}$	0.041	2.22	10.0**	0.129	–	–	–
Soil pH	–	–	–	−2.79	7.8**	0.100	–	–	–	−3.60	13.0***	0.156
S-signature	–	–	–	–	–	–	−1.96	3.8$^{(*)}$	0.053	–	–	–
CWM LDMC†	*−3.10*	*9.6***	*0.126*	–	–	–	–	–	–	**−4.14**	**17.1*****	**0.197**
CWM SSD†′ ¶	*2.84*	*8.1***	*0.108*	–	–	–	**1.66**	**2.8(*)**	**0.040**	–	–	–
Invasion status* T_{BP}	β_C 1.30 β_I 3.53	5.0*	0.069	–	–	–	–	–	–	–	–	–

Notes: CWM, community-weighted mean; T_{BP}, average temperature during the burial period; LDMC, leaf dry matter content; S-signature, mean abundance-weighted functional stress signature; SSD, stem-specific density; β_C, beta coefficient for control plots; β_I, beta coefficient for invaded plots. Models were run for rooibos percent mass loss, green tea percent mass loss, *Impatiens glandulifera* leaf percent mass loss, and plant available nitrogen (N). Standardized beta coefficients, test statistics (F), and semi-partial R^2_β are given for each retained predictor after model reduction. Values in bold indicate results for predictors including *I. glandulifera* trait values, and values in italics indicate results for predictors excluding *I. glandulifera* trait values. N = 98.

$^{(*)}P < 0.10$; $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$.

† Logarithm transformation.

§ Cube root transformation.

¶ Transformation only for predictor including *I. glandulifera* trait values.

RESULTS

Invasion-induced trait changes

Comparing the CWM trait values excluding *Impatiens glandulifera* traits showed that plant communities invaded by *I. glandulifera* were characterized by lower LDMC and SSD, and higher SLA across all sites, whereas plant height was not significantly affected (Table 2, Fig. 1). *Impatiens glandulifera* had significantly higher plant height ($\beta_0 = -6.45$, $F = 41.7$, $P < 0.001$) and SLA ($\beta_0 = -6.24$, $F = 39.0$, $P < 0.001$; Fig. 1a, d), and significantly lower LDMC ($\beta_0 = 10.01$, $F = 100.1$, $P < 0.001$) and SSD ($\beta_0 = 8.98$, $F = 80.7$, $P < 0.001$; Fig. 1b, c), than the CWMs of the co-occurring species, according to the community-invader trait differences intercept LMMs.

Invasion had no consistent effects on community composition of the co-occurring species ($\chi^2 = -0.075$, $F = 0.87$, $P = 0.77$ for invasion status constrain in the CCA analysis), nor did it affect species richness or S-signature of the co-occurring species. Invasion did nonetheless result in a significantly lower C-signature for invaded compared to uninvaded communities (Appendices S1 and S2). As expected, communities with high S-signature had traits reflecting low litter quality (high LDMC and SSD, low SLA; Table 2). Unexpectedly, however, a similar pattern occurred for communities with high C-signature (Table 2), potentially reflecting the invader-induced trait changes (simultaneously toward low C-signature and high litter quality). The C-signature was furthermore positively correlated to plant height. Leaf dry matter content, SSD, and plant height were furthermore positively related to each other and negatively related to SLA (Appendix S3). *Impatiens glandulifera* traits were less strongly linked, with a negative correlation between LDMC and SLA, and a positive correlation between SSD and plant height (Appendix S3).

Invasion and trait effects on litter decomposition and plant available nitrogen

As expected, rooibos decomposition (22.7% average mass loss) was much slower than that of green tea (59.9% average mass loss) and *I. glandulifera* leaves (66.4% average mass loss; Fig. 2). Rates of litter decomposition were furthermore positively correlated for the three litter types across all plots (Appendix S4). Rooibos mass loss was on average 6.1% higher for invaded communities compared to control communities, although this pattern did not occur for the central Norway study region (Table 3, Fig. 2a). While green tea decomposition did not differ significantly between invaded and control plots, *I. glandulifera* leaf decomposition was on average

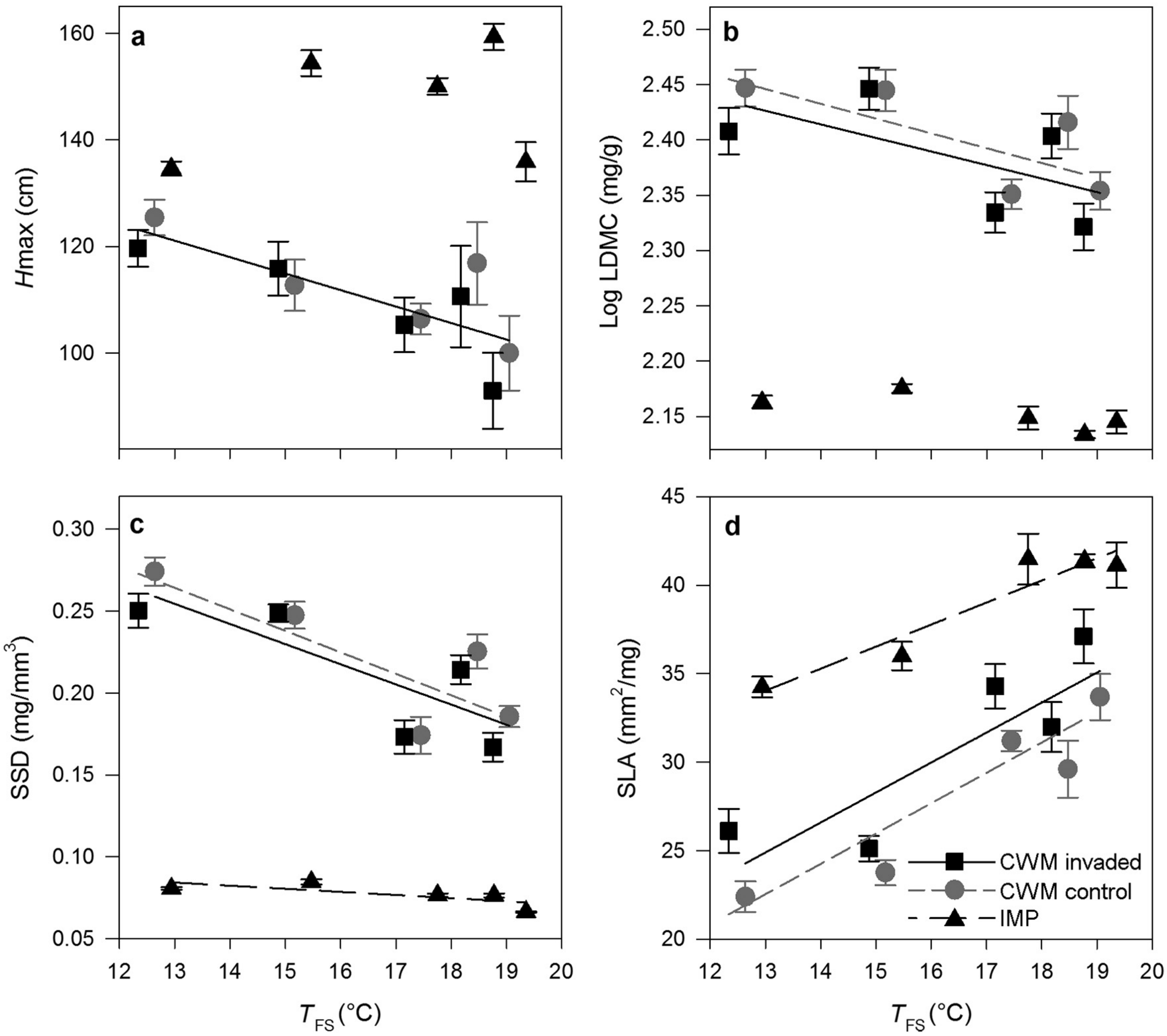

Fig. 1. Effects of mean temperature during the burial period (T_{BP}) on the community-weighted mean (CWM) traits of the invaded plots (black squares, continuous black line), the CWM traits of the control plots (gray circles, short dash gray line), and mean *Impatiens glandulifera* traits (black triangles, long dash black line). Separate graphs for (a) plant height, (b) leaf dry matter content (LDMC), (c) stem-specific density (SSD), and (d) specific leaf area (SLA). Note that CWM traits were calculated excluding *I. glandulifera* traits. Error bars are ± standard error. Regression lines given for significant patterns following the linear mixed models.

2.5% higher for invaded communities, although this difference was more pronounced for three of the five study regions (Table 3, Fig. 2c). Plant available nitrogen (N) was on average lower for invaded plots and decreased with increasing soil pH (Table 3).

Rooibos mass loss was strongly correlated with LDMC (negatively) and SSD (positively) for CWM values excluding *I. glandulifera*, explaining approximately 12.6% and 10.8% of the variation in mass loss, respectively (Table 3, Fig. 3). Because of strong collinearity between CWM LDMC and CWM SLA, both traits were equally good at predicting rooibos mass loss (using separate LMM models, results for CWM SLA not shown). Green tea mass loss was unrelated to any CWM trait, but was higher when buried underneath communities on low pH soils (Table 3). *Impatiens glandulifera* leaf decomposition, in turn, was higher for communities with low S-signature and high SSD

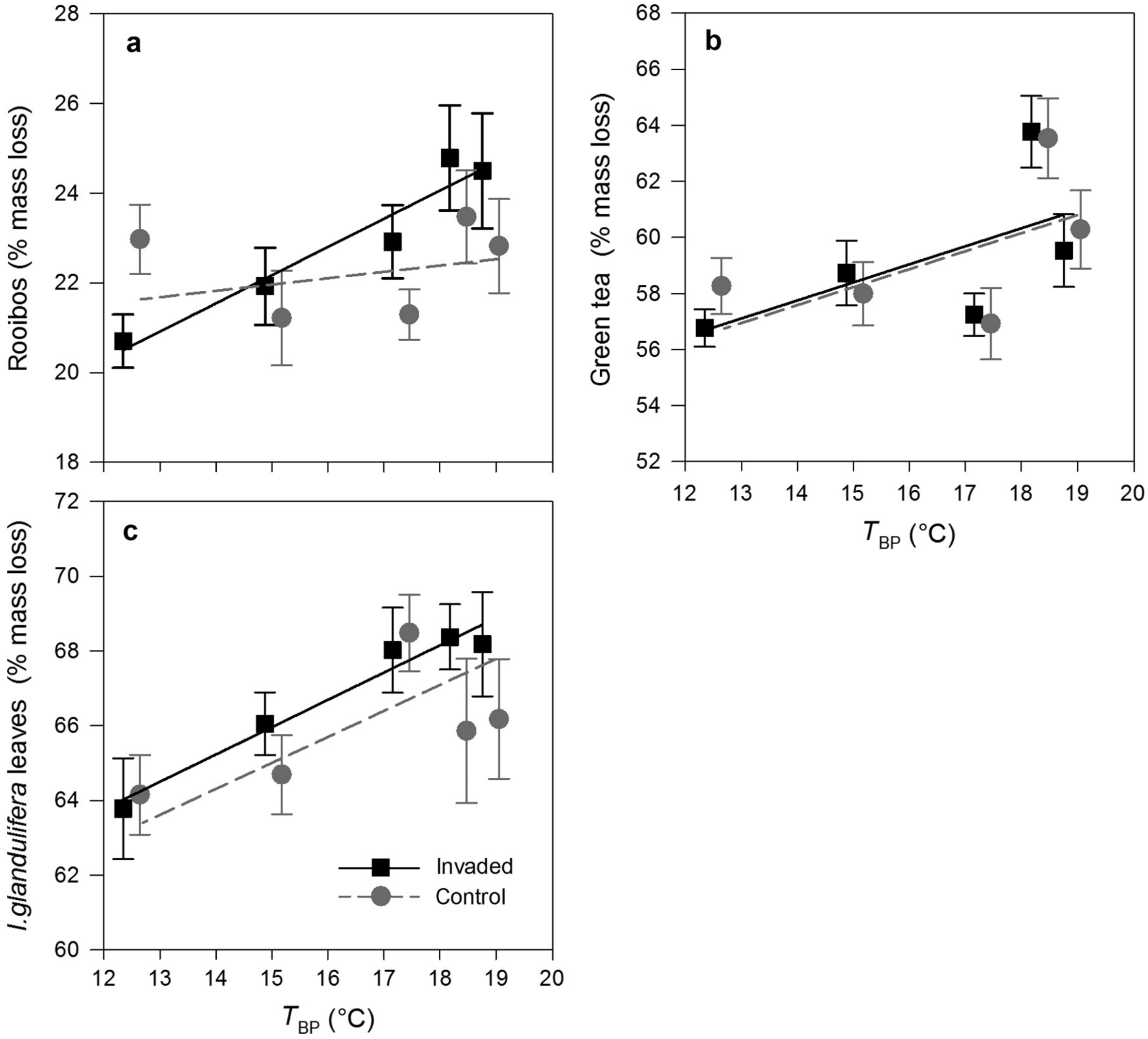

Fig. 2. Effects of mean temperature during the burial period (T_{BP}) on litter decomposition (percentage mass loss) of (a) rooibos mass loss, (b) green tea mass loss, and (c) *Impatiens glandulifera* leaf mass loss. Invaded plots are shown as black squares (continuous black line), and control plots as gray circles (short dash gray line). Error bars are ± standard error.

CWM values (including *I. glandulifera* traits). Plant available nitrogen (N) was furthermore negatively related to LDMC CWM values (including *I. glandulifera* traits; Table 3).

Latitudinal gradient effects

Variation along the latitudinal gradient was quantified using climatic and soil conditions, given their importance for the decomposition process. The five study regions varied in mean temperature (T_{BP}; 12.3–18.8°C) and in total precipitation (P_{BP}; 30–129 mm) during the burial period (Table 1). T_{BP} decreased significantly with latitude (Appendix S5), presenting a 6.5°C increase from the northernmost region (central Norway) to the southernmost region (Belgium) of the study gradient (Table 1). Increasing temperature along the gradient was furthermore associated with a decrease in P_{BP} and S-signature, and an increase in C-signature (Appendix S5). Although the range in soil pH was substantial (between 4.3 and 7.5), most variation occurred across

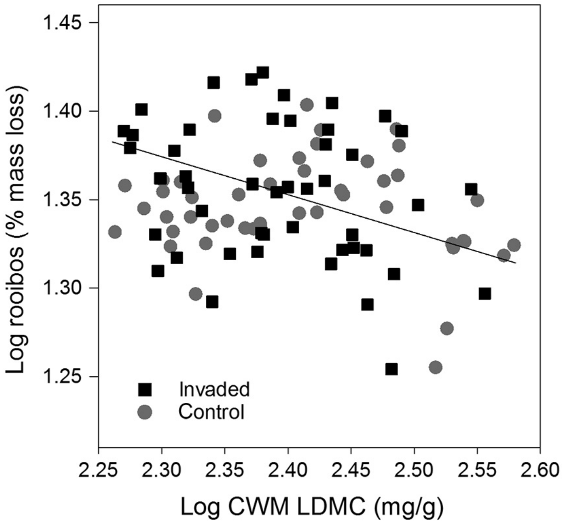

Fig. 3. Relationships between the rooibos mass loss and the community-weighted mean (CWM) leaf dry matter content (LDMC) excluding *Impatiens glandulifera* traits. Separate symbols for invaded plots (black squares) and control plots (gray circles). Note that rooibos mass loss and CWM LDMC were logarithmically transformed. Regression line is predicted for all plots from the linear mixed models.

populations within the same region, rather than across the latitudinal gradient (Appendix S5).

All CWM trait values were significantly related to T_{BP}, with an average decrease in plant height by 27%, LDMC by 3% and SSD by 49% and an increase in SLA by 32% from the coldest to the warmest study region (Table 2, Fig. 1). These temperature effects were independent of invasion effects for SLA trait variation. For LDMC and SSD on the other hand, trait differences between invaded and control communities were slightly more pronounced at low T_{BP} (marginally significant interaction term, Table 2). *Impatiens glandulifera* traits were also affected by climatic variation, with an average increase in SLA by 17% and a decrease in SSD by 22% from the coldest to the warmest study region, hence responding similarly as the CWM trait values (Table 2, Fig. 1). Both plant height and SSD also decreased with increasing P_{BP} (Table 2).

All three litter types decomposed faster in the warmer study regions, with a significant increase in percentage mass loss of 8.4% for rooibos, 5.0% for *I. glandulifera* leaves, and only a marginally significant trend for green tea (4.1%) along the studied temperature gradient (Table 3, Fig 2). Although rooibos mass loss increase with T_{BP} occurred for both invaded and control plots, a reversal of the invasion effect occurred in the coldest study region (central Norway), where mass loss of rooibos was higher in the uninvaded communities (significant interaction term; Table 3). Also noteworthy was the similarly (slightly) higher mass loss of green tea in uninvaded communities for the coldest study region (central Norway; Fig. 2b). Plant available nitrogen was not significantly affected by the climatic variation along the gradient.

DISCUSSION

Invasion shifted CWM trait composition toward more acquisitive traits and thus higher litter quality. Similarly, CWM trait composition shifted toward more acquisitive traits with increasing temperature along the latitudinal gradient. These changes resulted in increased litter decomposition rates of the labile litter fraction in invaded communities, a shift that was most evident in the warmer study regions. The changes occurred for standardized litter, suggesting an invader effect on the decomposition environment and/or community. Plant available nitrogen was unexpectedly lower in invaded communities, likely due to high nutrient uptake by *Impatiens glandulifera*. Meanwhile, the coldest, northernmost study region was characterized by a reversed effect of invasion on decomposition rates. Here, low litter quality and potential allelopathic effects of the invader resulted in reduced litter decomposition rates, suggesting a threshold temperature at which invader effects on litter decomposition turn positive.

Invasion-induced trait changes

Impatiens glandulifera had an impact on CWM trait values through two pathways. First, *I. glandulifera*'s trait values differed significantly from the CWM trait values, introducing more acquisitive plant traits (higher plant height and SLA, lower LDMC and SSD), and thus high-quality (leaf) litter to the community (Wright et al. 2004, Orwin et al. 2010). These trait differences have been previously observed for this species and for several other successful invading alien species and have been linked to invasion success (Leishman et al. 2007, van Kleunen et al. 2010; K. Helsen, *unpublished manuscript*). Secondly, the presence of *I. glandulifera* resulted in shifts in the CWM trait values for the co-occurring native species, again toward more acquisitive plant traits (higher SLA, lower LDMC and SSD; Wright et al. 2004). This shift was mainly driven by intraspecific trait changes within the community, since both species richness and community composition was largely unaffected by invasion. The absence of a strong effect of *I. glandulifera* on plant community composition of the co-occurring species is in agreement with the literature (Hulme and Bremner 2006). The observed community trait changes in invaded communities match the theoretically expected changes under increased competition for light and/or nutrients (Wright et al. 2004, Hodgson et al. 2011; K. Helsen, *unpublished manuscript*). Both invader effects seem to be synergistic, together resulting in an increase in the average community litter quality (Garnier et al. 2004, Quested et al. 2007, Finerty et al. 2016). Likewise, Aerts et al. (2017) found related shifts in functional leaf traits of co-occurring native plant species following invasion of *Prunus serotina*, resulting in higher litter quality.

Invasion and trait effects on litter decomposition

Invasion increased decomposition of the generally slowly decomposing rooibos litter, which is indicative of a potential increased decomposition rate of the labile litter fraction (Keuskamp et al. 2013). This was evident for all communities except the northernmost (coldest) study region. Differences in rooibos decomposition rate were furthermore strongly related to CWM leaf (LDMC and/or SLA) and stem (SSD) traits. Several studies have found CWM LDMC to be the best predictor of litter decomposability (Kazakou et al. 2006, Quested et al. 2007). This effect also seems to hold for standard litter decomposition in our study, with CWM LDMC (and/or CWM SLA) explaining 12.6% of the variation in rooibos mass loss. These results suggest that the shift toward acquisitive plant traits and associated higher litter quality can potentially modulate changes in the decomposer environment and/or community to a more bacterial-dominated soil community (Orwin et al. 2010, de Vries et al. 2012). This, in turn, can enhance the decomposition of standard litter (Scherer-Lorenzen 2008, McLaren and Turkington 2011, Yahdjian et al. 2017). The often observed increase in litter decomposition rates of native litter in the presence of alien litter might be driven by similar processes (Liao et al. 2008, Finerty et al. 2016). Note that the unexpected positive correlation between rooibos decomposition and CWM SSD suggests a more complex link between SSD and litter decomposition. Unlike the measured leaf (and stem) traits, plant height did not affect any of the litter decomposition variables.

Our results show no significant difference in green tea litter mass loss (and thus recalcitrant litter buildup) between invaded and control communities (Keuskamp et al. 2013). This was unexpected, since the observed faster decomposition of the labile fraction (rooibos) in invaded communities is theoretically expected to result in the buildup of a larger fraction of recalcitrant litter due to increased nitrogen-based litter stabilization (Berg 2000). Our results furthermore suggest that community traits had no significant effect on green tea mass loss in this study, with only pH explaining 10% of the green tea mass loss variation. This higher green tea mass loss on acidic soils could reflect a lower recalcitrant fraction in acidic soils, due to pH induced differences in decomposition rates and decomposer communities (fungal dominated in acidic soils; Hättenschwiler et al. 2005).

Similarly to rooibos mass loss, the high-quality *I. glandulifera* leaves decomposed faster in the invaded communities. This could suggest that decomposer effects following alien plant invasion are, at least partly, driven directly by the presence of invader litter (Finerty et al. 2016). The strong correlations between the rooibos mass loss and community traits excluding *I. glandulifera* traits, on the other hand, suggest that part of the observed invader decomposition effects is driven indirectly by changes in the community-level trait composition. A more detailed study of *I. glandulifera* litter decomposition is needed to ascertain whether *I. glandulifera* litter directly affects the decomposer environment and/or community. What is more, *I. glandulifera* litterbags were filled with dried leaf material, not leaf litter, potentially resulting in higher decomposition rates since nutrient resorption did not take place. However, *I. glandulifera* is an annual species, implying that any resorbed nutrients will eventually be returned to the soil as leaf or stem litter at the end of the growing season (Beerling and Perrins 1993, Dassonville et al. 2008).

Invasion and trait effects on plant available nitrogen

Invaded plots had consistently lower plant available nitrogen than control plots during the peak growing season. This is counterintuitive, since the faster litter decomposition in invaded plots is expected to increase soil nitrogen availability (Berg 2000). The observed pattern may reflect the intense nutrient uptake by *I. glandulifera*. Indeed, previous research has shown that *I. glandulifera* builds up large amounts of nitrogen-rich biomass (Dassonville et al. 2008). This could also explain the absence of stronger buildup of nitrogen-stabilized recalcitrant litter fractions (green tea mass loss) in the invaded plots.

Variation in nitrogen availability was furthermore related to community trait values including *I. glandulifera* traits, supporting the idea of a more direct effect of *I. glandulifera* on nitrogen availability. More specifically, the reduced nitrogen levels in invaded plots were most pronounced for communities characterized by low litter quality (i.e., high LDMC). The fast litter decomposition in plots with high litter quality likely releases higher amounts of nitrogen back into the soil, thus counteracting the competition induced reduction in available nitrogen. A more detailed study of soil nitrogen dynamics in relation to *I. glandulifera* litter decomposition could further elucidate these mechanisms (García-Palacios et al. 2016).

Latitudinal gradient effects

All CWM functional traits changed significantly along the latitudinal (6.5°C climatic) gradient. The warmest location (Ghent) was characterized by more exploitive traits, likely due to the increased relative importance of competition effects (cf. the stress gradient hypothesis, Bertness and Callaway 1994). Given the community leaf traits, community litter quality is likely to be higher toward the warmer end of the gradient (Cornwell et al. 2008). *Impatiens glandulifera* traits followed a similar pattern along the studied gradient, albeit less pronounced. Litter decomposition of all three litter types was also faster in warmer sites. Although higher temperatures typically result in faster decomposition rates due to increased microbial activity (Hättenschwiler et al. 2005), the observed climatic effects are likely partly enhanced by the litter quality effects on decomposer environment and/or community, thus supporting our climatic gradient hypothesis. The absence of any precipitation effects on litter decomposition is likely due to the fact that this species mainly occurs on wet riparian soils, thus limiting potential decomposition rate reduction due to low precipitation (Beerling and Perrins 1993).

Interestingly, the positive effect of *I. glandulifera* presence on litter decomposition did not occur for the coldest study region (central Norway), where both rooibos mass loss and, to a lesser extent, green tea mass loss were higher for control plots. This strongly suggests that invader effects on litter decomposition are not solely driven by invader-induced community trait shifts. Instead, *I. glandulifera* might negatively affect decomposition directly through microclimate (shading) effects (Ruckli et al. 2013) or allelopathy effects on the (fungal) decomposer communities (Ruckli et al. 2014, Suseela et al. 2016). Although these negative effects would occur everywhere along the studied gradient, these effects might be stronger at high latitudes, where decomposer communities are most likely to temperature limited due to low air temperature in shaded locations. Additionally, the positive impact of *I. glandulifera* on litter quality might not be sufficient in this area to increase decomposition rates, since *I. glandulifera* had lower litter quality here compared to more southern locations. The balance between negative and positive invader effects on decomposition might then tip toward a net positive effect on litter decomposition when temperature exceeds a certain threshold. Evaluation of *I. glandulifera* effects on litter decomposition further north along its invaded European range could provide additional insight in these processes.

CONCLUSIONS

This study illustrates how functional trait changes toward acquisitive traits can help explain invader-induced changes in ecosystem functions such as increased litter decomposition. These trait changes furthermore partly explained the shift in invader effects along the gradient. This study clearly illustrates how adopting a functional trait-based framework can provide additional understanding of invader effects and their potential context-dependency. The inconsistent invader effects along the studied latitudinal gradient in this study furthermore support the context-dependence of invader effects, thus illustrating the importance of large-scale studies of invader effects (Kramer et al. 2012, Stotz et al. 2017). This context-dependence of invader effects furthermore suggests that care should be taken when predicting impacts of invasive species on ecosystem functions across large spatial scales or when extrapolating local findings to the full invaded range.

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