



# Invasive knotweed has greater nitrogen-use efficiency than native plants: evidence from a $^{15}\text{N}$ pulse-chasing experiment

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Received: 24 October 2018 / Accepted: 13 August 2019 / Published online: 22 August 2019  
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## Abstract

Habitats with fluctuating resource conditions pose specific challenges to plants, and they often favor a small subset of species that includes exotic invaders. These species must possess a superior ability to capitalize on resource pulses through faster resource uptake or greater resource-use efficiency. We addressed this question in an experiment with invasive knotweed, a noxious invader of temperate ecosystems that is known to benefit from nutrient fluctuations. We used stable isotopes to track the uptake and use efficiency of a nitrogen pulse in competition pairs between knotweed and five native competitors. We found that nitrogen pulses indeed promoted knotweed invasion and that this is explained by a superior efficiency in turning the taken-up extra nitrogen into biomass, rather than capturing an overproportional share of the nitrogen. Thus, temporary increases in nutrient availability might help knotweed to invade natural environments, such as river banks or nitrogen-polluted margins and wastelands, where nutrient fluctuations occur. Our experiment shows that resource-use efficiency can drive invasion under fluctuating resource conditions, and that stable isotopes help to understand these processes.

**Keywords** Biological invasions · Fluctuating resources · Interspecific competition · Invasiveness · Stable isotopes

## Introduction

Competition for resources is one of the most important drivers of plant community structure (Grace and Tilman 1990; Grime 1979). In temperate ecosystems, nutrients are often limiting (Keddy 2007; Maestre et al. 2009; Harpole et al. 2011), and for a species to be successful, it must be able to capture resources quickly when they become available (Yang et al. 2008; Craine and Dybzinski 2013), use the resources efficiently (Chapin 1980), or, ideally, do both. It is important to consider these two dimensions of competitive ability if we

want to understand what enables some species to become dominant.

When a plant community is exposed to episodes of increased nutrient availability, those species will benefit that can quickly accelerate nutrient uptake (James and Richards 2006). Such rapid physiological responses are then often followed by morphological responses such as altered root systems that help to maintain higher levels of nutrient uptake. Once resources are captured, the benefits can be further increased by a greater nutrient use efficiency (Chapin 1980; Mamolos et al. 1995; Lu et al. 2013), e.g., because of a more economic root–shoot allocation (Clark and Zeto 2000) or increased carbon-to-nitrogen ratio in tissues (Aerts and Chapin 2000). Because of these mechanisms, greater resource availability generally promotes some species over others (Berg and Ellers 2010) and often leads to a decrease in community diversity (Harpole et al. 2016) and habitats strongly dominated by only few species.

Many of the plant species that become abundant in habitats characterized by regular disturbance and nutrient inputs are invasive exotics (Daehler 2003; Leishman and Thomson 2005). One explanation for this is provided by the so-called ‘fluctuating resource hypothesis’ (Davis et al. 2000) which postulates that during nutrient fluctuations, the nutrient

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Communicated by Casey P. terHorst.

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uptake capacity of whole communities may be exceeded, providing temporary resource surpluses, and thus windows of opportunity for invasion. In addition, invasive species often appear to profit more—relative to their native competitors—from increased nutrient availability (Blumenthal 2006; Blumenthal et al. 2009). To explain this, researchers have invoked either a greater general phenotypic plasticity in response to increased nutrient availability (Funk 2008; Dawson et al. 2012; Davidson et al. 2011) or an overall higher resource-use efficiency (Shen et al. 2011) of the invaders. However, much of the previous work has been either simple nutrient addition experiments or field studies that related invader abundance to the nutrient conditions in different habitats, whereas more detailed studies following the dynamics of resource uptake are so far rare. Therefore, we still do not understand which aspects of nutrient uptake matter most for the success of invasive plants: their overall capacity for nutrient uptake, their speed of response when additional nutrients become available, or their efficiency in turning extra nutrients into biomass, and thus a competitive advantage.

A particularly useful tool in experimental studies of plant nutrient dynamics is stable isotopes (Dawson et al. 2002) which enable tracing plant resource uptake in real time and to study the speed and efficiency of use of a particular resource. In competition studies, stable isotopes allow researchers to track the partitioning of resources among different individuals or species, and thus to assess the intensity and asymmetry of competition (Kahmen et al. 2006). However, so far, stable isotopes have been rarely used to study resource competition between invasive and native plants (but see Littschwager et al. 2010; Werner et al. 2010; Qing et al. 2015; Huangfu et al. 2016).

One of the world's most successful plant invaders is Japanese knotweed (*Reynoutria japonica*), a Polygonaceae native to Eastern Asia and invasive in temperate Europe and North America after being introduced as ornamental in the nineteenth century (Bailey and Connolly 2000). It is a tall perennial forb which mainly reproduces vegetatively through rhizomes. In its exotic range, the species is often very dominant and forms monospecific stands by outcompeting virtually all native vegetation. From a previous experimental study, we know that this dominance is promoted by variable nutrient supply: when competing against a community of European species, knotweed success was tripled when nutrients were supplied in irregular pulses rather than in a more regular fashion (Parepa et al. 2013). What we do not know is whether the advantage from variability came from a superior ability to uptake the nutrients from the individual pulses or a higher efficiency of using the uptake, or maybe a combination of both. As invasive knotweed is one of the most noxious plant invaders and causes substantial ecological and economic damage (Invasive Species Specialist Group

2016; Rumlerová et al. 2016), it is important to understand its mechanisms of invasion success, including its superior ability to exploit fluctuating nutrient conditions.

Here, we used stable nitrogen isotopes to follow the fates of single nutrient pulses in competition between invasive knotweed and native species. In a pot experiment, we paired knotweed with five native European species that are common in the habitats invaded by knotweed, and we exposed these pairs to nutrient pulses enriched with stable nitrogen isotopes. To determine uptake and efficiency of resource use, we measured nutrient uptake and dominance of each competitor at three different time points during a month. We expected that (1) invasive knotweed will benefit more than natives from the nutrient pulse, and (2) this might be due to a faster uptake, more efficient conversion to biomass, or both.

## Methods

To study nutrient competition between knotweed and native plants, we set up pots in which knotweed was planted pairwise with five native European species that are all common in the habitats invaded by knotweed: *Geranium robertianum*, *Geum urbanum*, *Silene dioica*, *Symphytum officinale*, *Urtica dioica*. All are fast-growing perennials from mesic and nutrient-rich habitats and also reproduce clonally, except for *Geranium* which has an annual or biennial life history and rarely clonal. The native species were germinated in advance from seeds provided by a commercial producer of wild seeds (Rieger-Hoffmann GmbH; Blaufelden, Germany) while *Reynoutria japonica* rhizomes were harvested from a live collection of clones grown in an experimental garden for several years, with the taxonomic identities of all clones verified through molecular methods.

For each native species–knotweed pair, we filled 30 1.5 L pots with a standard potting substrate (Florabella Universal, Klasmann-Deilmann, Geeste, Germany) and planted one native seedling in each pot. One week later, when all seedlings had established well, we additionally planted one piece of knotweed rhizome approximately 8 mm thick and 10 cm long, with two intact nodes, into each pot. We then allowed the plants to grow, and we continuously monitored plant height and leaf chlorophyll (closely correlated with leaf N) using a chlorophyll meter (SPAD 502Plus, Konica Minolta, Osaka, Japan). Within about 1 month, the plants stopped growing and showed clear signs of nutrient depletion. At this point, we measured the height of each of the two plants in every pot, and we then applied a single nutrient pulse in each pot, using potassium nitrate ( $\text{KNO}_3$ ) labeled with  $^{15}\text{N}$  at a  $^{14}\text{N}:$  $^{15}\text{N}$  ratio of 7:1. There were two experimental treatments: a control treatment with a nutrient level equivalent to  $0.2 \text{ g N m}^{-2}$ , and a pulse treatment with  $2 \text{ g N m}^{-2}$ . Out of the 15 pots per knotweed–native combination in

each treatment, five pots were harvested 1 day after the pulse, another five after 1 week, and the remaining five after 1 month. At each harvest, we cut the aboveground biomass and carefully washed and separated the belowground biomass of each competitor in each pot, dried all biomass samples at 70 °C for 48 h and weighed them. We used these data to calculate knotweed dominance as the biomass fraction that knotweed achieved within each pot, separately for above- and belowground biomass.

### Isotope analysis

For the chemical analyses, we fine-ground all weighed biomass samples using a ball mill (Retsch MM 400, Retsch GmbH, Haan, Germany). On a 4 mg subsample, we determined the nitrogen content and the  $^{15}\text{N}$  enrichment in the tissues as the proportion of  $^{15}\text{N}/^{14}\text{N}$  compared to a standard ( $\delta^{15}\text{N}$  vs. Air-N<sub>2</sub>). The measurement of  $\delta^{15}\text{N}$  and the %N content value was performed using a Flash EA 1112 Series elemental analyzer (Thermo Italy, Rodano, Italy) coupled to a Finnigan MAT Delta<sup>plus</sup>XP isotope ratio mass spectrometer (Finnigan MAT, Bremen, Germany) via a 6-port valve (Brooks et al. 2003) and a ConFlo III (Werner et al. 1999). We then used these data to calculate, separately for above- and belowground biomass, the absolute amounts of nitrogen originating from the pulses that each competitor had taken up in each pot.

### Data analysis

For our strategy of data analysis, and to disentangle nitrogen uptake from nitrogen-use efficiency, it was important to consider the temporal dynamics of nitrogen uptake and biomass production, based on the three harvest time points. We found a strong  $^{15}\text{N}$  enrichment signal already 1 day after the pulse. After 1 week,  $^{15}\text{N}$  recovery had increased to 60% in the control treatment, and to 40% in the pulse treatment, but it did not further increase after that (Supporting Information Fig. S1). Thus, the  $^{15}\text{N}$  uptake took place entirely within the first few days. The dynamics of biomass production were different: there was little change, and hardly any difference between the treatments, within the first week, but after 1 month, the plants from the pulse treatment were much larger than the control plants (Supporting Information Fig. S2). Thus, the biomass responses to the nutrient treatments almost took place entirely after the first week. Based on this information, we split the dataset by harvest time and used the data from the first week for understanding nitrogen uptake, and the data from the 1 month after the pulse for understanding biomass responses and thus nitrogen-use efficiency.

To get an idea of the competitive success of knotweed in the different treatments and species pairs, we analyzed

the proportion of knotweed in aboveground biomass after 1 month. We use the *cbind* function in R to create a binary response variable by concatenating the knotweed and native competitor aboveground biomass. Then we fitted a generalized linear model with quasi-binomial distribution in which we tested the effect of nutrient treatment (control vs. pulse), competitor species (five levels), and their interaction. To account for differences in initial size, we used the ratio between the initial heights of knotweed and competitor as covariate. We fitted identical models for above- and belowground dominance data. Both showed similar effect sizes for species and nutrient treatment, but for the belowground data, the standard errors were always larger (see Supporting Information Fig. S3), presumably because root cleaning was difficult and imprecise, and because the belowground biomass included the planted rhizomes. We, therefore, restricted further analyses to aboveground data.

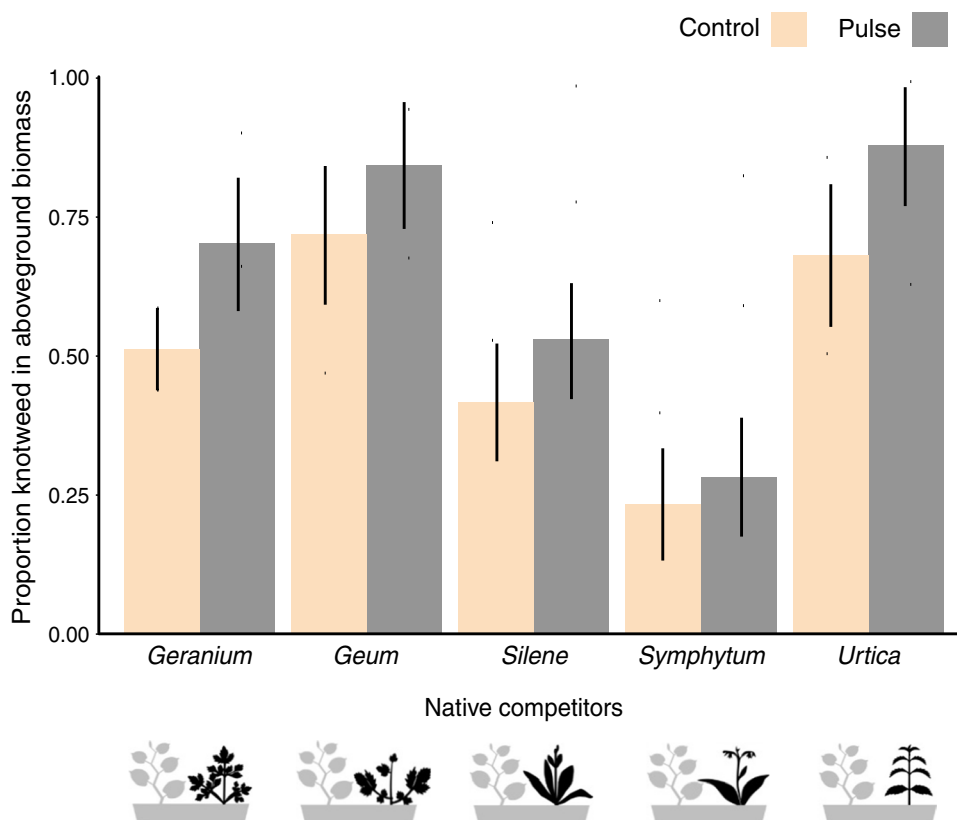
To understand observed changes in the relative dominance of knotweed, we further analyzed a series of linear mixed models for individual plant data in which we tested the effects of nutrient treatment (control vs. pulse), origin (invasive knotweed vs. native competitor), and competitor species nested within origin, and their interactions, on (1) plant final aboveground biomass, (2) nutrient uptake (absolute amount of  $^{15}\text{N}$  taken up per gram biomass), and (3) nutrient-use efficiency (final biomass per final nitrogen content). To account for the non-independence of data from the same pot, we fitted the pot identity as a random effect in all three analyses. To account for differences in initial size, for the biomass data, we first fitted a linear model in which the plant height standardized within each species was the explanatory variable. We used the residuals from this model as response variable in the main analyses.

All data analyses were done in R (R Core Team 2016). We used the base package, *lme4* (Bates et al. 2015) and *lmerTest* (Kuznetsova et al. 2017), and did all figures with the *ggplot2* package (Wickham 2009).

## Results

Invasive knotweed benefited more than native competitors from the nutrient addition. One month after the pulse treatment, the proportion of knotweed in aboveground biomass increased by 15% (Fig. 1; nutrient treatment:  $\chi^2 = 64.9$ ,  $P < 0.001$ ) against all competitor species (nutrient treatment  $\times$  competitor species:  $\chi^2 = 3.58$ ,  $P = 0.32$ ), regardless of whether they were weak or strong competitors. In the control treatment, the knotweed constituted about half of the aboveground biomass in competition with *Geranium* or *Silene*, while it had a much greater biomass share in competition with *Geum* and *Urtica*, but was inferior to *Symphytum* (competitor species:  $\chi^2 = 52.9$ ,  $P < 0.001$ ).

**Fig. 1** Proportion of knotweed in aboveground biomass when competing pairwise with five native European species 1 month after a nutrient pulse equivalent to either 0.2 g N m<sup>-2</sup> (control) or 2 g N m<sup>-2</sup> (pulse). The bars represent least square means  $\pm$  1 SE estimated from a generalized linear model (see “Methods” for details). Color version of this figure is available online



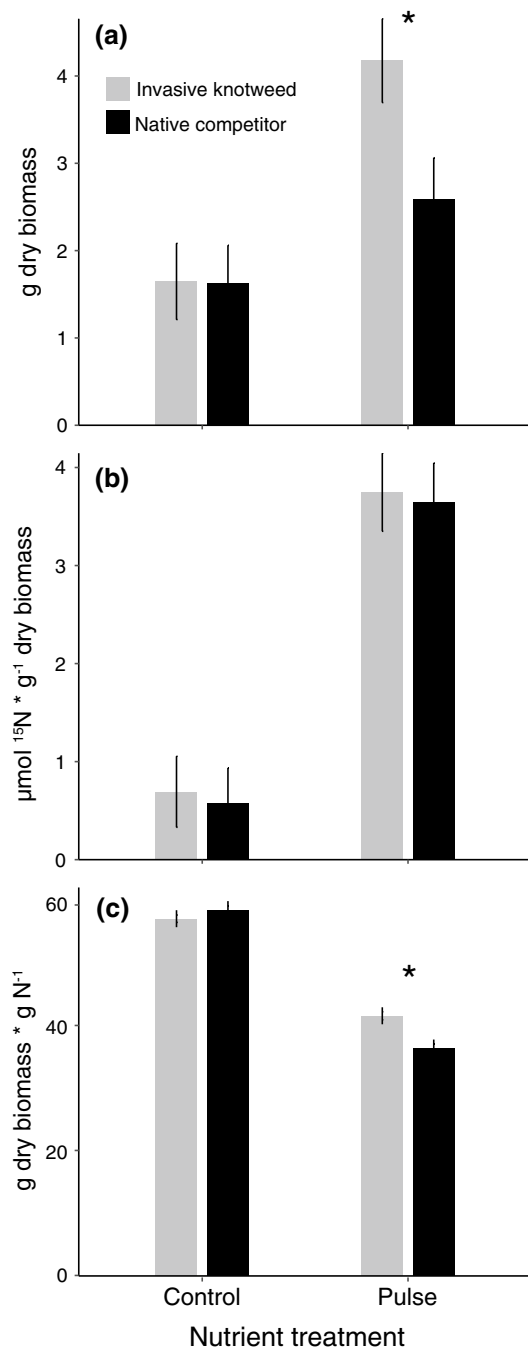
The analyses of individual plant data showed no evidence that knotweed has a faster nutrient uptake than native competitors, while it has a superior nitrogen-use efficiency when more nutrients are available. As expected, the pulse treatment increased biomass and nitrogen uptake of both competitors, while decreasing their nitrogen-use efficiency (Fig. 2; significant main effect of nutrient treatment in all three response variables in Table 1). Interestingly, the biomass responses to the nitrogen pulse were stronger for knotweed than for native competitors (Fig. 2a; significant origin by treatment interaction for aboveground biomass in Table 1). This increase was not related to differences in nitrogen uptake which remained equal between knotweed and natives in both treatments (Fig. 2b; no effect of origin or nutrient treatment  $\times$  origin in Table 1). The gain in biomass may be explained instead by knotweed's superior nitrogen-use efficiency, which, in the pulse treatment was 10% higher than the one of native competitors (Fig. 2c; significant nutrient treatment  $\times$  origin in Table 1).

## Discussion

Invasive knotweed is one of the most damaging plant invaders in temperate ecosystems, and it is known to benefit from temporary increases in nutrient supply. Here, we examined the role of potential mechanisms governing the increase

in dominance following a nutrient pulse. In a competition experiment, we used stable isotopes to track the uptake and use efficiency of a nitrogen pulse in pairs of knotweed and native plants. We found that knotweed is profiting from nutrient pulses relative to the native species, but not because it is able to capture an overproportional share of the resource, but because it possesses a superior ability to turn the taken-up extra resources into biomass growth, and thus competitive dominance.

As we predicted, in the pulse treatment, where resource availability was higher, the dominance of invasive knotweed increased. This result adds to previous findings that many invasive species profit from a larger nutrient supply (e.g., Daehler 2003; Blumenthal et al. 2009; van Kleunen et al. 2018) or from a large nutrient pulse (Liu and van Kleunen 2017). However, in contrast to most of the previous studies, our experiment focused on rather short time scales and followed resource uptake and growth responses after 1 day, 1 week, and 1 month. Our results at least partly explain why knotweed is becoming more dominant under fluctuating resource conditions (Parepa et al. 2013): if after every nutrient pulse knotweed gains relatively more biomass than its competitors, then this advantage may be progressively amplified by subsequent events in a fluctuating resource environment (Davis et al. 2000). Still, even with only a single resource pulse, an advantage gained early in the growing season could propagate through priority effects (Harper



**Fig. 2** **a** Aboveground biomass, **b** nitrogen uptake, and **c** nitrogen-use efficiency of invasive knotweed (gray bars) or native competitor (black bars) following a nutrient application equivalent to either  $0.2 \text{ g N m}^{-2}$  (control) or  $2 \text{ g N m}^{-2}$  (pulse). Nitrogen uptake was measured 1 week after the pulse, while aboveground biomass and nitrogen-use efficiency were measured 1 month after the pulse. The bars represent least square means  $\pm 1$  SE estimated from mixed effects models (see “Methods” for details). Stars indicate a significant difference between origins within a nutrient treatment

1961; Connell and Slatyer 1977; Fukami et al. 2005) and give the invader a critical competitive edge. For knotweed, the gain of biomass dominance is particularly relevant as its invasion success is almost exclusively based on vegetative growth and reproduction (Bailey et al. 2009), with viable offspring regenerating from rhizome and stem fragments (Gowton et al. 2016). More generally, if such abilities are more common among successful invasive plants, this may explain why invaders often show stronger priority effects than native plants (e.g., Wilsey et al. 2015; Stuble and Souza 2016). It is interesting that, in our experiment, the greatest relative biomass advantage was gained by the smaller knotweed plants in the experiment, indicating that nutrient pulses may indeed help the invaders during early phases of establishment, and to turn the tide to its advantage.

To better understand a species’ resource competitive ability, it is useful to discriminate between its ability to take up a particular resource and the efficiency by which it can use this resource (Bridgham et al. 1995; Craine and Dybzinski 2013). In our experiment, invasive knotweed was not better than native competitors at capturing the nitrogen pulse. The isotope content in the tissues 1 week after the pulse was equal for knotweed and its competitors, regardless of their identity. This is in contrast to our predictions and to some other studies which found superior resource capture in other plant invaders (e.g., Funk 2013; Gioria and Osborne 2014).

While within the first days after a nitrogen pulse the biomass of a plant is likely little affected yet by the pulse, and rather determines nitrogen uptake, the situation should reverse after some time, when biomass changes will reflect previous nitrogen uptake. We found that 1 month after the nitrogen pulse, the relative nitrogen content was lower in knotweed biomass than in the biomass of the native plants. Similarly, to its competitors, knotweed increased the nitrogen concentration in aboveground biomass where more nutrients were available, but it did so to a lesser extent. This finding corroborates evidence from several previous studies that found invaders to possess superior resource-use efficiency (Funk and Vitousek 2007; Shen et al. 2011; Osone et al. 2014; Ens et al. 2015; Qing et al. 2015). The ability to maintain a relatively higher nitrogen efficiency when more nitrogen is available—which is equivalent to producing more biomass with the same total amount of nitrogen—may be explained by a higher activity of the enzyme nitrate reductase as found by Chmura et al. (2016). Since, for large knotweed stands in the field, leaf nitrogen content was similar to neighboring vegetation (Aguilera et al. 2010), we can expect that the superior nitrogen-use efficiency we see in our experiment may play be important in the early stages of invasion, when knotweed is gaining dominance.

Overall, compared to its competitors, knotweed did not have a superior capture ability, instead it was able to turn the extra resources more efficiently into biomass and thus

**Table 1** Analysis of variance of the aboveground biomass, nitrogen uptake, and nitrogen-use efficiency of individual plants in competition pairs of invasive knotweed vs. five native European species

Source of variation	df	Aboveground biomass			Nitrogen uptake			Nitrogen-use efficiency		
		MS	F ratio	P value	MS	F ratio	P value	MS	F ratio	P value
Nutrient treatment (Tr)	1	13.83	9.29	0.003**	37.41	10.54	0.002**	36.03	133.40	<0.001***
Origin (O)	1	24.50	16.44	<0.001***	0.19	0.05	0.823	0.78	2.91	0.095
Species [O] (Sp)	4	8.55	5.74	<0.001***	2.64	0.74	0.656	0.65	0.30	0.962
Tr×O	1	8.56	5.74	0.018*	0.09	0.03	0.862	1.55	5.75	0.021*
Tr×Sp [O]	4	1.01	0.66	0.710	1.57	0.44	0.893	0.06	0.23	0.983

For each response variable, we fitted a linear mixed model and tested the effects of nutrient treatment (control: 0.2 gN m<sup>-2</sup> or pulse: 2 gN m<sup>-2</sup>), origin of competitor (invasive knotweed or native competitor), competitor species (*Geranium robertianum*, *Geum urbanum*, *Silene dioica*, *Symphytum officinale*, or *Urtica dioica*) nested within origin, and their interactions, while pot (=identity of competing pair) was included as random effect. \*\*\* $P < 0.001$ , \*\* $P < 0.01$ , \* $P < 0.05$ ,  $P < 0.1$

competitive success. The native competitors in our experiment were all fast-growing species common in resource-rich habitats and they are invasive elsewhere or considered weeds (Randall 2017). Even when growing against such strong competitors that capture nutrients equally well, invasive knotweed gained from an increase in resources.

Taken together, our findings demonstrate, again, that invasive knotweed is promoted by fluctuating resource conditions. The observed mechanism could help knotweed to increase in abundance and eventually dominate native communities particularly in environments, such as river banks or nitrogen-polluted margins and wastelands, where temporal fluctuations in nutrient availability occur. More generally, superior resource uptake or greater nutrient-use efficiency may explain why many invasive plant species benefit from increased nutrient availability (Davis and Pelsor 2001; Davidson et al. 2011; Dawson et al. 2012). Our study shows that an invader does not necessarily need to be good in both, and that the use of stable isotopes can help to disentangle and understand these processes better.

**Acknowledgements** We thank Nina Buchmann for advice and discussion on the experimental design, Yvonne Zürcher and Carole Adolf for assistance with measurements and processing the biomass samples, and the Botanical Garden in Bern for providing space for the experiment. We thank Casey terHorst and three anonymous reviewers for their helpful comments on previous versions of the manuscript. This work was supported by the Swiss National Science Foundation (SNF Project No. 122408 to OB) and the German Research Foundation (DFG Project PA 2608/2-1 to MP).

**Author contribution statement** OB and MP formulated the idea and conceived the experiment. MP, OB, AK, RW, and MF designed the experiment. MP and AK performed the experiment and RW performed the isotope analysis. MP analyzed the data. MP and OB wrote the manuscript; all other authors provided editorial advice.

## Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflict of interest.

**Ethical approval** This article does not contain any studies with human participants or animals performed by any of the authors.

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