Altered ecosystem carbon and nitrogen cycles by plant invasion: a meta-analysis

Chengzhang Liao[1,2], Ronghao Peng[1], Yiqi Luo[1,2], Xuhui Zhou[2], Xiaowen Wu[2], Changming Fang[1], Jiakuan Chen[1] and Bo Li[1]

[1]Coastal Ecosystems Research Station of Yangtze River Estuary, Ministry of Education Key Laboratory for Biodiversity Science and Ecological Engineering, The Institute of Biodiversity Science, Fudan University, Shanghai 200433, China; [2]Department of Botany and Microbiology, University of Oklahoma, Norman, OK 73019, USA

Author for correspondence:
Bo Li
Tel: +86 21 65642178
Fax: +86 21 55664990
Email: bool@fudan.edu.cn

Summary

• Plant invasion potentially alters ecosystem carbon (C) and nitrogen (N) cycles. However, the overall direction and magnitude of such alterations are poorly quantified.

• Here, 94 experimental studies were synthesized, using a meta-analysis approach, to quantify the changes of 20 variables associated with C and N cycles, including their pools, fluxes, and other related parameters in response to plant invasion.

• Pool variables showed significant changes in invaded ecosystems relative to native ecosystems, ranging from a 5% increase in root carbon stock to a 133% increase in shoot C stock. Flux variables, such as above-ground net primary production and litter decomposition, increased by 50–120% in invaded ecosystems, compared with native ones. Plant N concentration, soil NH_4^+ and NO_3^- concentrations were 40, 30 and 17% higher in invaded than in native ecosystems, respectively. Increases in plant production and soil N availability indicate that there was positive feedback between plant invasion and C and N cycles in invaded ecosystems.

• Invasions by woody and N-fixing plants tended to have greater impacts on C and N cycles than those by herbaceous and nonN-fixing plants, respectively. The responses to plant invasion are not different among forests, grasslands, and wetlands. All of these changes suggest that plant invasion profoundly influences ecosystem processes.

Key words: carbon and nitrogen pools and fluxes, litter quality, meta-analysis, plant invasion, soil nitrogen availability.

Introduction

Biological invasion is a significant element of global change (Vitousek *et al.*, 1997; Mack *et al.*, 2000; Pimentel *et al.*, 2000). The invasion rate of exotic species is predicted to increase rapidly in coming decades, largely because of the expansion of global trade, agriculture and many other human activities (Vitousek *et al.*, 1997; Mack *et al.*, 2000; Weber & Li, in press). Plant invasion not only threatens biodiversity and stability of native ecosystems, but also potentially affects ecosystem functioning and processes (Vitousek *et al.*, 1997; Gordon, 1998; Mack

et al., 2000; Ehrenfeld, 2003). Carbon (C) and nitrogen (N) cycles are fundamental components of ecosystem functioning and processes. Therefore, there is an urgent need to understand how C and N cycles respond to plant invasion.

Plant invasion can alter various components of ecosystem C and N cycles. Many studies (Harcombe *et al.*, 1993; Lett *et al.*, 2004; Wilsey & Polley, 2006) have shown that net primary production (NPP) increased in the invaded ecosystems relative to the native ecosystems. Allison & Vitousek (2004) and Rothstein *et al.* (2004) have found that litter of invasive species decomposed more rapidly than that of native species,

which was associated with the higher litter quality of the invasive species. Greater ecosystem C and N stocks have been observed in the invaded than in native ecosystems (Vitousek & Walker, 1989; Hibbard *et al.*, 2001). In addition, Ehrenfeld *et al.* (2001) have shown that soils have higher rates of net N mineralization and nitrification, and higher NH_4^+ and NO_3^- concentrations under canopies dominated by invasive species than those under the native species, suggesting that plant invasion might have positive feedback to further invasion.

However, other studies have shown that plant invasion can have negative effects on C and N cycles. For example, Jackson *et al.* (2002) observed a C loss from a grassland ecosystem invaded by woody plants. Johnson & Wedin (1997) have reported that soil N stock decreased with an invasion of grass into dry tropical forests. Windham & Ehrenfeld (2003) have found that above-ground litter of the invasive *Phragmites australis* decomposed more slowly than that of the native *Spartina patens*. Thus, different results among experimental studies indicate that a comprehensive understanding of whole ecosystem response to plant invasion remains elusive.

The high variability among the experimental results can stem from the differences in life form between invasive woody and herbaceous species. For example, Ehrenfeld *et al.* (2001) have shown that the invasive woody *Berberis thunbergii* had a greater shoot biomass than the native *Vaccinium pallidum*, but that the invasive herbaceous *Microstegium vimimeum* had a smaller shoot biomass than *V. pallidum* in New Jersey, USA. The variability can also result from the functional differences in the mechanism of N fixation between invasive N-fixing and nonN-fixing plants. For example, invasion by *Spartina alterniflora* in which N fixation is associated with the epiphytic community on standing dead shoots enhanced soil C stock in the Yangtze estuarine wetlands of China (Liao, 2007), whereas invasion of the nonN-fixing *Agropyron cristatum* decreased total soil N concentration at the northern edge of the Great Plains (Christian & Wilson, 1999). Additionally, the variability can come from the differences in ecosystem types such as forests, grasslands, and wetlands. For example, in the Hawaiian forests, litter decomposition rate was higher for the invasive *Myrica faya* than for the native *Metrosideros polymorpha* (Vitousek & Walker, 1989). In tidal wetlands of New Jersey, however, litter decomposition rate of the invasive *P. australis* was as high as that of the native *S. alterniflora* after 2 yr of decomposition (Windham *et al.*, 2004). In the grasslands of eastern Kansas, litter decomposition rate was lower for the invasive *Juniperus virginiana* than for the native *Andropogon gerardii* (Norris *et al.*, 2001). Therefore, to generalize the effects of plant invasion on C and N cycles, it is imperative to synthesize results from independent studies across species and ecosystems.

Several syntheses have been conducted to explore the effects of plant invasion on C and N cycles. Vitousek *et al.* (1997) reviewed the studies of *M. faya* invasion in Hawaii Volcanoes National Park, and Gordon (1998) reviewed the studies of plant invasions in Florida. Both of them concluded that invasive species had the potential to alter C and N cycles of invaded ecosystems. Ehrenfeld (2003) reviewed 79 studies on plant invasion, and listed the direction of change in C and N cycles in response to the invasion of exotic species in individual studies, and brought forward a concept that there could be positive feedbacks between plant invasion and C and N cycles. However, these syntheses used a qualitative approach, and cannot provide an overall direction and magnitude of C and N cycles in response to plant invasion across species and ecosystems. Therefore, quantitative analysis is still necessary for an evaluation of ecosystem response to plant invasion.

In this study, 94 experimental studies were synthesized, using a meta-analysis approach, to quantify the changes in C and N cycles in response to plant invasion. The meta-analysis has the potential to obtain a general pattern of invasion effects on C and N cycles from independent studies (Osenberg *et al.*, 1999). A response ratio (RR, the ratio of the mean value of a concerned variable in an invaded ecosystem to that in a native one) is used here as an index of the magnitude of invasion effect (Hedges *et al.*, 1999; Luo *et al.*, 2006). More specifically, the meta-analysis was used to address the following three questions. First, to what extent were ecosystem C and N stocks altered by plant invasion, in comparison with native ecosystems? Second, how did ecosystem C and N processes respond to plant invasion? Third, was there any positive feedback between plant invasion and C and N cycles in invaded ecosystems?

Materials and Methods

Data sources

To avoid bias in publication selection, the following five criteria were set for the inclusion of data related to C and N cycles with reference to plant invasion; (i) the invasive species examined were vascular higher plants; (ii) the ecosystems contained both invasive and native plant species; (iii) the studies directly compared invaded ecosystems dominated by invasive species with the corresponding native ones in terms of C and N cycles; (iv) the experimental studies were conducted in the field or in laboratories, but free of significant disturbances (e.g. fire and herbivory) or treatments (e.g. fertilization, clipping, warming, light, etc.) – otherwise, the disturbance or treatment events, rather than the interaction of invasive species with ecosystem types, would have altered C and N cycles (Ehrenfeld, 2003); (v) where experiments involved reciprocal transfers of invasive and native species, data were only collected of invasive species in invaded ecosystems and native species in native ecosystems.

Data were collected from 94 published experimental studies (see Supplementary material, Text S1). In total, 20 variables associated with C and N cycles were examined in invaded and native ecosystems (Table S1). Pool variables included C and N stocks in shoots, roots, litter, soils and soil microbes. Flux variables included above-ground net primary production (ANPP), litter decomposition rate, the net mineralization and

nitrification rate of N in the soil. Descriptive variables of C and N pools and fluxes included plant N concentration, litter N and lignin concentrations, litter C : N and lignin : N ratios, and soil NH_4^+ and NO_3^- concentrations. For other variables, such as below-ground net primary production, litter N stock, the rates of plant-associated N fixation and N loss, there were not enough data for a meta-analysis. All the data used here were extracted from figures and tables in published papers. For each of the 20 variables, the mean (M), standard error (SE) or standard deviation (SD) or confidence interval (CI), and sample size (n) in both invaded and native ecosystems were extracted. The variables associated with soils were measured at a depth of 10 cm within an original range of 5–100 cm. Soil C and N stocks were obtained through multiplying total soil C and N concentrations by an assumed soil bulk density of 1.0 g cm^{-3} when the studies provided only total soil C and N concentrations. Soil organic C stock was not distinguished from total soil C stock because the change of soil organic C stock resulting from plant invasion almost represented the change of total soil C stock responding to plant invasion (Jackson *et al.*, 2002). If the temporal dynamics of a target variable was presented in original studies, the averaged mean ($\overline{M}$) and the averaged standard error ($\overline{SE}$) of the variable were estimated as:

$$\overline{M} = \sum_{i=1}^{j} M_i / j \qquad \text{Eqn 1}$$

$$\overline{SE} = \sqrt{\dfrac{\sum\limits_{i=1}^{j} SE_i^2 (n_i - 1) n_i}{\left(\sum\limits_{i=1}^{j} n_i - 1\right) \sum\limits_{i=1}^{j} n_i}} \qquad \text{Eqn 2}$$

where j is the sampling times (≥ 2), M_i, SE_i and n_i were mean value, standard error and sample size on the ith sampling date, respectively.

The constructed database consisted of 1045 lines of entries, which were used to compute the response ratio and then to explore the general pattern of effects of plant invasion on C and N cycles. Additionally, to examine the role of life form and N fixation, invasive species were grouped into woody and herbaceous plants, and into N-fixing plants, including both symbiotic and associative fixers (e.g. *Prosopis*, *Acacia*, *Myrica* and *Spartina*) and nonN-fixing plants, respectively. Ecosystems were grouped into forests, grasslands and wetlands. We further explored the effects of invasive species with different life forms and functional groups of N fixation on C and N cycles, and the effects of plant invasion on C and N cycles in forests, grasslands and wetlands.

Analysis

The method of meta-analysis used in this study followed previous studies by Hedges *et al.* (1999) and Luo *et al.* (2006).

Plant invasion was regarded as treatment in invaded ecosystems relative to native ecosystems. M, SE or SD or CI, and n extracted from both of invaded and native ecosystems in individual studies were used to compute the logarithm of response ratio (RR), the weighted response ratio (RR$_{++}$) and the 95% CI of RR$_{++}$. Homogeneity tests to check whether or not removing one RR from a series of RRs for a given variable would significantly affect the results of comparisons followed Gurevitch & Hedges (1993). If yes, the RR was excluded from the calculation of RR$_{++}$. The percentage of change in a variable was estimated by $(e^{RR_{++}} - 1) \times 100\%$.

If the 95% CI values of RR$_{++}$ for a variable did not overlap between the invasive woody and herbaceous species, between the invasive N-fixing and nonN-fixing plants, or among forests, grasslands and wetlands, the effects of plant invasion on the variable were significantly different between two life forms, two functional groups of N fixation of invasive species, or among three types of ecosystems. If the 95% CI values of RR$_{++}$ overlapped, Student's t-test was used to further examine whether or not the difference was significant between or among them.

Frequency distributions of RR ($n > 30$) were plotted to validate the results from the meta-analysis by a Gaussian function (i.e. normal distribution) (Luo *et al.*, 2006):

$$y = ae^{-\frac{(x-\mu)^2}{2\sigma^2}} \qquad \text{Eqn 3}$$

where x is the mean of RR in individual intervals, y is the frequency (i.e. the number of RR values) in an interval, a is a coefficient representing the expected number of RR values at $x = \mu$, μ and σ^2 are the mean and variance of the frequency distributions of RR, respectively.

Results

The response ratios (RR$_{++}$) of 20 variables related to C and N cycles examined by the meta-analysis were all significantly different from zero ($P < 0.001$ for all variables; Fig. 1). The frequency distributions of 14 variables ($n > 30$) followed a normal distribution of Gaussian function ($P < 0.05$ for all) (Figs S1, S2), and the 14 μ-values from the model of Gaussian function were all consistent with the corresponding RR$_{++}$ (Figs S1 and S2 vs Fig. 1).

Plant invasion enhanced C and N pool sizes in plants, soils and soil microbes (Table 1). Averaged C stocks in shoots, roots, litter, soils and soil microbes increased by 133, 5, 49, 7 and 34%, respectively, in invaded ecosystems in comparison with native ecosystems (Table 1). Averaged N stocks in shoots, roots, soils and soil microbe stocks were 86, 112, 19 and 26% higher in invaded than in native ecosystems, respectively (Table 1). In invaded ecosystems, for C pools, the percentage increases in both roots and soils were lower than those in shoots, litter and soil microbes (all $P < 0.001$). For N pools, the percentage increases in plants were higher than
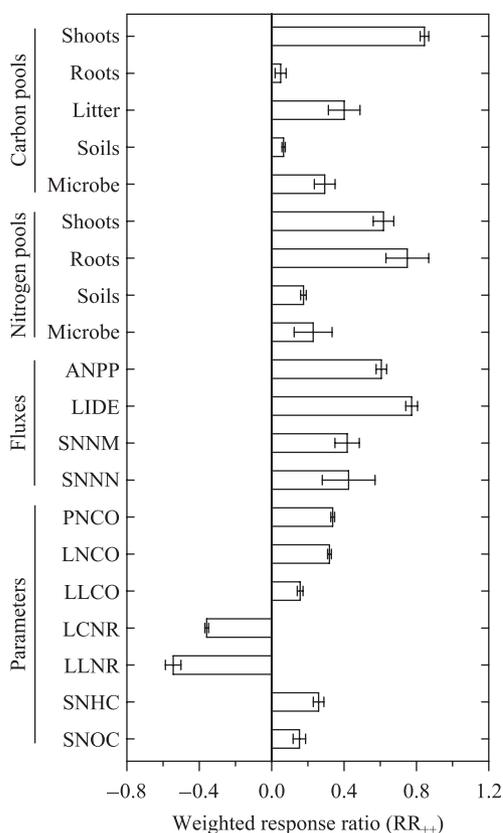
Fig. 1 Weighted response ratio (RR_{++}) of 20 variables related to carbon and nitrogen cycles in response to plant invasion. Bars represent $RR_{++} \pm 95\%$ confidence intervals. The vertical line was drawn at RR = 0. ANPP, above-ground net primary production; LIDE, litter decomposition; SNNM, soil net N mineralization; SNNN, soil net N nitrification; PNCO, plant N concentration; LNCO, litter N concentration; LLCO, litter lignin concentration; LCNR, litter C : N ratio; LLNR, litter lignin : N ratio; SNHC, soil NH_4^+ concentration; SNOC, soil NO_3^- concentration.

Table 1 Percentage of change of 20 variables related to carbon and nitrogen cycles in response to plant invasion

Variable	Percentage change $(e^{RR_{++}} - 1) \times 100\%$	n
Carbon pools		
Shoots	132.71 ± 2.38	84
Roots	5.15 ± 3.07	60
Litter	49.31 ± 9.14	16
Soil	6.86 ± 0.91	83
Microbe	34.12 ± 5.88	14
Nitrogen pools		
Shoots	85.63 ± 5.84	37
Roots	111.66 ± 12.55	7
Soil	19.25 ± 1.57	88
Microbe	25.81 ± 11.06	12
Fluxes		
ANPP	83.40 ± 2.95	42
LIDE	116.80 ± 3.28	58
SNNM	51.80 ± 6.91	58
SNNN	53.11 ± 15.70	27
Parameters		
PNCO	40.18 ± 1.06	86
LNCO	37.70 ± 1.06	92
LLCO	17.08 ± 1.63	57
LCNR	−30.15 ± 1.03	44
LLNR	−41.96 ± 4.40	16
SNHC	29.68 ± 2.98	87
SNOC	16.58 ± 3.47	77

Percentage of change is represented as the mean ± 95% confidence intervals.
ANPP, above-ground net primary production; LIDE, litter decomposition; SNNM, soil net N mineralization; SNNN, soil net N nitrification; PNCO, plant N concentration; LNCO, litter N concentration; LLCO, litter lignin concentration; LCNR, litter C : N ratio; LLNR, litter lignin : N ratio; SNHC, soil NH_4^+ concentration; SNOC, soil NO_3^- concentration.

those in soils and soil microbes in invaded ecosystems (all $P < 0.001$).

Above-ground net primary production, rate of litter decomposition, and rates of net mineralization and nitrification of N in soils were 83, 117, 52 and 53% higher in invaded than in native ecosystems, respectively (Table 1). Plant N concentrations, N and lignin concentrations in litter were 40, 38, 17% higher in invasive plants than in native ones, respectively (Table 1), but litter C : N and lignin : N ratios were 30 and 42% lower, respectively (Table 1). The corresponding values for soil NH_4^+ and NO_3^- concentrations were 30 and 17% higher (Table 1).

For the 20 variables evaluated in this study, the absolute values of 17 RR_{++} were higher for invasive woody species than for herbaceous ones (all $P < 0.05$) (Fig. 2a, Table S2). The rest of the RR_{++} values under invasion of woody species were lower than those of herbaceous species, respectively (all $P < 0.001$). For 16 of the 20 variables, the absolute values of RR_{++} were

higher for N-fixing invaders than for nonN-fixing ones (Fig. 2b; Table S2). For most of the 20 variables, invasions of both herbaceous and nonN-fixing plants also had significant impacts on C and N cycles in invaded ecosystems, compared with native ecosystems (Fig. 2a,b; Table S2). Forests, grasslands, and wetlands all responded significantly to plant invasion in relation to C and N cycles, and their responses were similar (Fig. 2c, Table S2).

Discussion

Methodological considerations

As in most similar studies, the published studies used here could have a bias because the studies with strong effects of plant invasion on C and N cycles might have been more frequently reported (Gurevitch & Hedges, 1999). Unfortunately, such bias is difficult to evaluate in a meta-analysis because of the lack of sufficient published data. The data sets collected in our
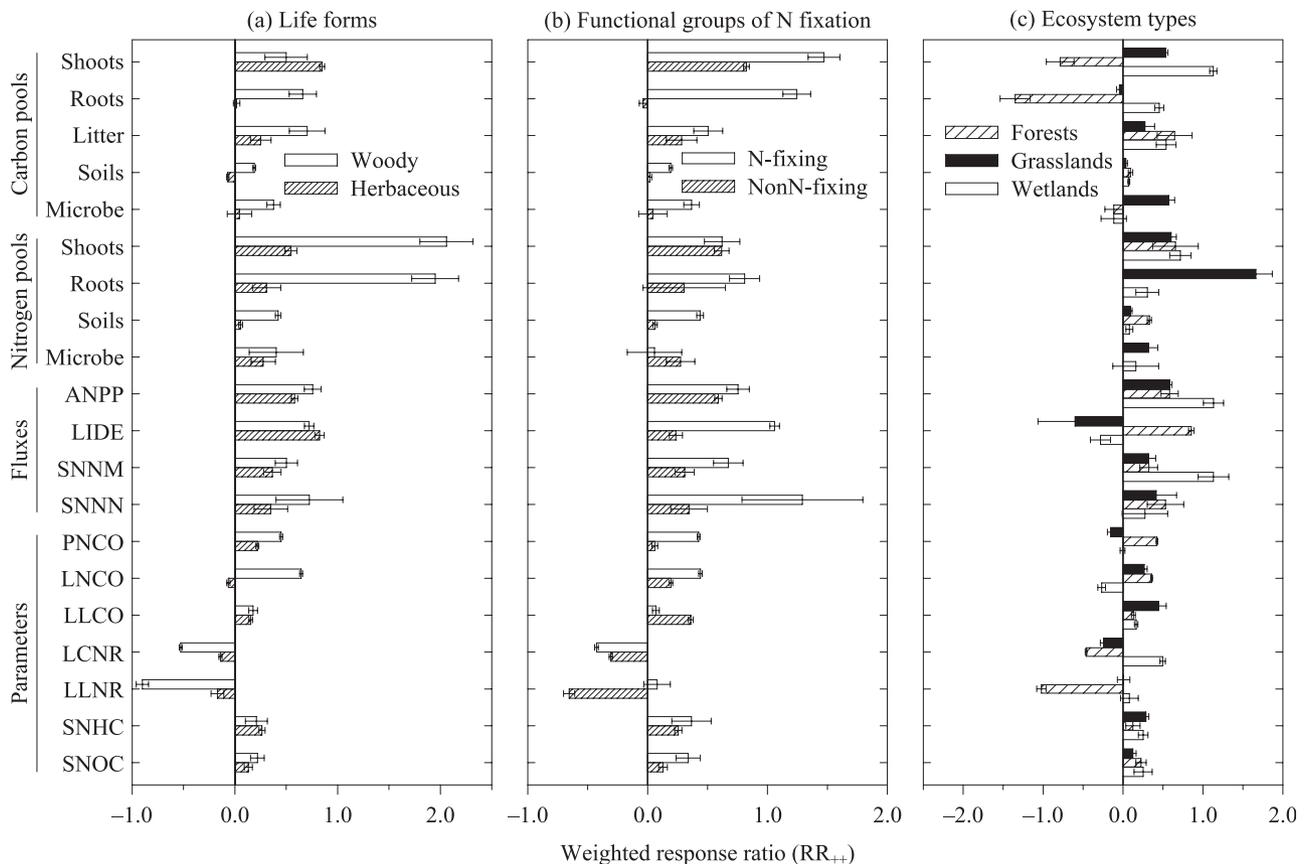
New
Phytologist

Fig. 2 Weighted response ratios (RR$_{++}$) of 20 variables related to carbon and nitrogen cycles under plant invasion with two life forms (a), two functional groups of N fixation (b), and in three ecosystem types (c). Bars represent RR$_{++}$ ± 95% confidence intervals. The vertical lines were drawn at RR = 0. See Supplementary material, Table S2 for details. ANPP, above-ground net primary production; LIDE, litter decomposition; SNNM, soil net N mineralization; SNNN, soil net N nitrification; PNCO, plant N concentration; LNCO, litter N concentration; LLCO, litter lignin concentration; LCNR, litter C : N ratio; LLNR, litter lignin : N ratio; SNHC, soil NH$_4^+$ concentration; SNOC, soil NO$_3^-$ concentration.

study might have come from regions where ecologists have conducted studies on the invasion for many years, for example, on the Hawaiian islands (Vitousek & Walker, 1989; Baruch & Goldstein, 1999; Hughes & Uowolo, 2006), while many other invaded regions have not attracted such attention from ecologists. This may cause uncertainties in the evaluation of the impacts of plant invasion. Furthermore, extrapolating the results from experimental studies, based on small-scale plot manipulations to an ecosystem scale, may also result in uncertainties. Sampling methods might also have been different from one study to another; for instance, the soil samples for determining the size of soil C pool were harvested up to a depth of 100 cm in the study of Liao (2007), but shallower than this depth in many other studies. In addition, the value of RR$_{++}$ can be sensitive to the additions/deletions of published studies if the volume of the data set constructed from selected studies for a variable is not large enough (Gurevitch & Hedges, 1999). Lastly, the change of a given variable may not be consistent with that of another in response to plant invasion; for example, the percentage of increase in N stock in shoots

should have been higher than that of C stock in shoots because of the increase in plant N concentration in response to plant invasion (Table 1). This could be caused by the different sets of data in computation of RR$_{++}$ in the meta-analysis. However, together with the modeling of Gaussian distribution of RR, the method of meta-analysis offered a powerful statistical analysis to quantify the changes in C and N cycles in response to plant invasion. Thus, these uncertainties were unlikely to change the general patterns obtained from the present study.

Enhancement of C and N processes

Plant invasion stimulated ANPP by 83% in invaded ecosystems compared with native ecosystems (Table 1). The increase in ANPP could result primarily from differences in ecophysiological traits such as specific leaf area and net photosynthetic rate between native and invasive species. Baruch & Goldstein (1999) showed that a sample of 30 invasive species, as a group, had a higher specific leaf area and a higher net photosynthetic

rate than a sample of 34 native species in Hawaii. Similar conclusions have also been drawn from other studies (Durand & Goldstein, 2001; Allison & Vitousek, 2004; Liang *et al.*, 2006). Invasive species have also been shown to have longer growing seasons than native species: the growing season of the invasive *S. alterniflora* was 50–80 d longer than that of the native *P. australis* and *Scirpus mariqueter* in estuarine wetlands in the Yangtze estuary, China (Liao, 2007). Through a combination of ecophysiological traits, invasive species may have the capacity to assimilate more C into ecosystems than native species.

Plant invasion increased litter decomposition rate by 117% in invaded ecosystems in comparison with native ecosystems (Table 1), which is consistent with many experimental studies (Allison & Vitousek, 2004; Rothstein *et al.*, 2004). The increase can be explained by the differences in plant N concentration and litter quality between invasive and native species. The invasive species had generally higher plant and litter N concentrations, and lower litter C : N and lignin : N ratio than the native species (Table 1), which primarily accounted for the higher decomposition rate in invaded ecosystems (Vitousek & Walker, 1989; Witkowski, 1991; Allison & Vitousek, 2004; Rothstein *et al.*, 2004). The high decomposition rate in invaded ecosystems suggests that plant invasion can accelerate ecosystem nutrient cycling processes.

Rates of soil net N mineralization and nitrification were, respectively, 52 and 53% higher in invaded ecosystems than in native ones. As with ANPP, the increases in soil N mineralization and nitrification could arise from ecophysiological differences between native and invasive species (Hibbard *et al.*, 2001; Ehrenfeld *et al.*, 2001; Windham & Ehrenfeld, 2003). Potential traits include NPP, plant and litter biomass, plant and litter N concentrations, and litter C : N ratio. The greater ANPP, plant and litter biomass, higher plant N concentration, and higher litter N concentration and lower litter C : N ratio (Table 1) could all lead to a higher rate of soil net N mineralization and nitrification. Additionally, the increases in soil net N mineralization and nitrification could also result from invasive species with N-fixing ability, for example, *M. faya* invasion in Hawaiian forests (Vitousek & Walker, 1989).

Together with N-rich litter and rapid litter decomposition, the high rates of soil N mineralization and nitrification could lead to increases in soil NH_4^+ and NO_3^- concentrations, which increase soil N availability (Svejcar & Sheley, 2001). These patterns were correspondingly reflected by the increases in soil NH_4^+ and NO_3^- concentrations in invaded ecosystems (Table 1).

Increases in ecosystem C and N stocks

Our meta-analysis demonstrates that plant invasion increased C pools, including those in shoots, roots, litter, soils and soil microbes (Table 1). The increase in ecosystem C stock can be attributed to the increase in plant production. On average,

ANPP in our analysis increased by 83% in invaded ecosystems in comparison with native ecosystems (Table 1), showing that invasive species assimilated more C via photosynthesis into plants and soils than native species (Arneth *et al.*, 1998). As a consequence, plant invasion enhanced C accumulation into invaded ecosystems.

Nitrogen pools, including plants, soils and soil microbes (Table 1), increased under plant invasion. Ecosystems have three important processes that can lead to increased N stocks in invaded ecosystems. First, increase in root biomass of invasive plants (Table 1) presumably resulted from an expansion of root systems. The larger root systems might take up N from soil zones which the roots of native species cannot exploit (Luo *et al.*, 2006). Second, the increase in ANPP in invaded ecosystems (Table 1) enhanced C input into the soils, providing more carbohydrates for soil microbes with N fixation (Knops *et al.*, 2002). Luo *et al.* (2006) showed that increase in C input into ecosystems promoted a significant increase in ecosystem N stock. Third, increase in soil microbial biomass C and N (Table 1) could stimulate net N accumulation in invaded ecosystems relative to native ones (Chapin *et al.*, 2002; Knops *et al.*, 2002). The review by Ehrenfeld (2003) also showed that soil microbial biomass N increased in eight out of 10 cases in response to plant invasion. The N stock in natural ecosystems has been built up over centuries to millennia before plant invasion occurred (Vitousek, 2004). The increase in ecosystem N stock suggests that plant invasion can rapidly alter the long-term dynamics of N cycles.

The percentage increase in C stock in plants was higher than that in soils in response to plant invasion (Table 1). Increase in plant C stock could result directly from the increase in plant production. Although there was much C input into soils as a result of the greater ANPP in invaded ecosystems (Table 1), C sequestration into soils might be limited by litter decomposition (Richter *et al.*, 1999). Therefore, the accumulation rate of soil C stock was smaller than that of plant C stock because of the increased decomposition rate in invaded ecosystems relative to native ones.

The percentage increase in soil N stock was higher than that in soil C stock in response to plant invasion (Table 1). Such changes in the soil could be explained by litter quality. Litter N concentration was 38% higher and litter C : N ratio was 30% lower in invaded ecosystems than in native ones (Table 1). Consequently, N release into soil was proportionally greater than C input into soil during litter decomposition (Hobbie, 1996; Christian & Wilson, 1999; Chapin *et al.*, 2002). The change in soil C and N pools suggests that plant invasion could alter the elemental composition in soils.

Variability in response

High variability in ecosystem C and N pools, fluxes and their parameters in response to plant invasion was observed in our meta-analysis (Fig. 1; Figs S1, S2). This variability reflects

diverse responses of various C and N processes to the invasion of a given species, and points to the need for caution in predicting response based on the mean effects.

Ecophysiological traits are well known to be a driving factor in regulating C and N cycles (Chapin *et al.*, 2002). The differences in ecophysiological traits are often species-specific between invasive and native species (Baruch & Goldstein, 1999; Durand & Goldstein, 2001). For example, the RR values of foliar phosphorus concentration varied from –0.55 to 0.88; and the RR values of specific leaf area varied from –0.22 to 0.66 when the invasive fern tree (*Sphaeropteris cooperi*) was compared with the native fern trees in Hawaiian forests (Allison & Vitousek, 2004). Thus, such species-specific differences contribute to the variability in response of C and N cycles to plant invasion. The variation in responses of C and N cycles, both from invasive woody species to invasive herbaceous species (Fig. 2a) and from N-fixing invaders to nonN-fixing ones, could be explained by the species-specific differences in ecophysiological traits. Our results demonstrate that, relative to the native species, the percentage increases in ecophysiological variables, such as ANPP, plant N concentration and litter biomass, were higher for invasive woody than for herbaceous species, and for invasive N-fixing than for nonN-fixing plants.

Similar responses of C and N cycles among forests, grasslands and wetlands to plant invasion (Fig. 2b) could be related to the interactions of invasive species with various ecophysiological traits and ecosystem types. For most variables examined in this study, each of the three types of ecosystem had both invasive woody and herbaceous species and invasive N-fixing and nonN-fixing plants. Thus, any differential effects resulting from the differences in ecophysiological traits between invasive woody and herbaceous species, invasive N-fixing and nonfixing plants might have been swamped.

Certainly, there are many other factors that may affect the variability of the response of C and N cycles to plant invasion. These factors include length of invasion history (Hughes & Uowolo, 2006), season (Christian & Wilson, 1999), and precipitation (Jackson *et al.*, 2002). Christian & Wilson (1999) showed that, when *A. cristatum* invaded northern Great Plains, soil N availability was not different between invaded and native ecosystems sampled in June, but significantly lower in invaded than in native ecosystems sampled in both August and October Jackson *et al.* (2002) found a clear negative relationship between precipitation and change in soil organic C when grasslands were invaded by woody species, with a C gain in dry sites and a C loss in wet sites. How these factors affect the patterns of C and N cycles in response to plant invasion deserves further evaluation.

Implications

Our analyses show that plant invasion significantly enhanced ANPP and soil NH_4^+ and NO_3^- concentrations across invasive woody and herbaceous species, invasive N-fixing and nonN-fixing plants, and in forests, grasslands and wetlands (Fig. 2, Table S2). The enhanced ANPP was important to ecosystem C accumulation, which could further stimulate N input into ecosystems because of linked C and N cycles in terrestrial ecosystems (Chapin *et al.*, 2002), although sufficient experimental data were not found to examine the impacts of plant invasion on rates of N fixation (three cases) and loss (no data available). The increased NH_4^+ and NO_3^- concentrations show that soil N availability was enhanced in invaded ecosystems relative to native ecosystems. The increased soil N availability could stimulate plant growth (Pastor *et al.*, 1984; Vitousek & Howarth, 1991). More importantly, soil microbial biomass C and N significantly increased under plant invasion (Fig. 1). Therefore, all of these changes support a conceptual framework in which there were positive feedbacks between plant invasion and C and N cycles in invaded ecosystems (Fig. 3).

The ecosystem-based feedbacks have several ecological implications. First, the feedbacks acted either to accelerate the invasion or to stabilize the invasive species once the invasion was under way. These feedbacks largely explained why invasive plant species could expand so rapidly in the new habitats, which makes the restoration of native ecosystems difficult. Second, the feedbacks show that plant invasion could stimulate fixation of a large amount of atmospheric CO_2 into the invaded ecosystem for a long time. In this respect, it is different from the opinion that plant invasion has detrimental effects on ecosystems (Mack *et al.*, 2000; Pimentel *et al.*, 2000). Thus, it would be too early to make a comprehensive evaluation for impacts of plant invasion on ecosystem functioning and processes. Third, the feedbacks indicate that plant invasion had a series of effects on C and N cycles, which could in turn alter the biogeochemical cycles of other elements in invaded ecosystems because C and N are key macroelements. Additionally, the feedbacks show that the impact of plant invasion on soil N gain or loss could be an important research priority, given that N stocks in plants, soils and soil microbes were significantly altered in invaded ecosystems in comparison with native ecosystems.

Our results from the meta-analysis clearly show an overall direction and magnitude of the response of C and N cycles to plant invasion. Plant invasion significantly enhanced ecosystem C and N pools, and increased C and N fluxes in invaded ecosystems relative to native ecosystems. Plant invasion increased both litter quality and soil N availability in invaded ecosystems. These changes show that there were positive feedbacks between plant invasion and C and N cycles in invaded ecosystems. Invasions by woody and N-fixing species usually produced greater impacts on C and N cycles than those by herbaceous and nonN-fixing species, respectively. Forests, grasslands and wetlands responded similarly to plant invasion in relation to C and N cycles. All of these changes suggest that plant invasion profoundly altered ecosystem functioning and processes.
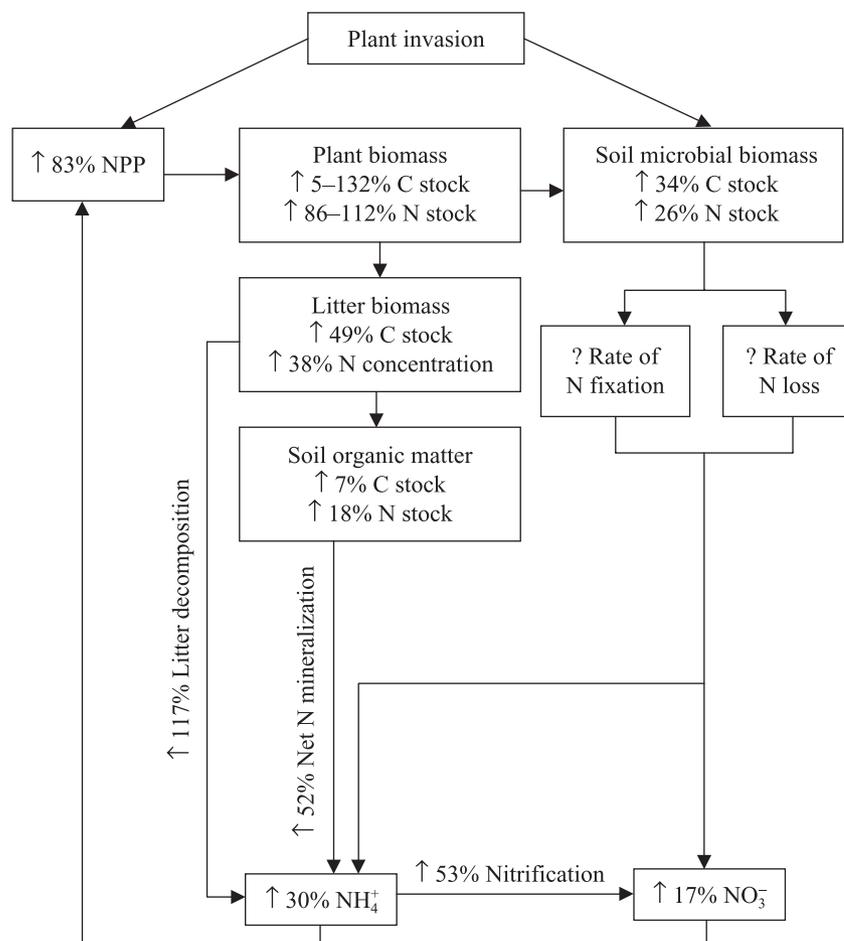
Fig. 3 Potential positive feedbacks between plant invasion and carbon and nitrogen cycles in invaded ecosystems. ↑, positive response to plant invasion; ?, not clear for the response to plant invasion. NPP, net primary production.

Acknowledgements

References

Allison SD, Vitousek PM. 2004. Rapid nutrient cycling in leaf litter from invasive plants in Hawai'i. *Oecologia* **141**: 612–619.

Arneth A, Kelliher FM, McSeveny TM, Byers JN. 1998. Net ecosystem productivity, net primary productivity and ecosystem carbon sequestration in a *Pinus radiata* plantation subject to soil water deficit. *Tree Physiology* **18**: 785–793.

Baruch Z, Goldstein G. 1999. Leaf construction cost, nutrient concentration, and net CO_2 assimilation of native and invasive species in Hawaii. *Oecologia* **121**: 183–192.

Chapin IIFS, Matson PA, Mooney HA. 2002. *Principles of Terrestrial Ecosystem Ecology.* New York, NY, USA: Springer.

Christian JM, Wilson SD. 1999. Long-term ecosystem impacts of an introduced grass in the northern Great Plains. *Ecology* **80**: 2397–2407.

Durand LZ, Goldstein G. 2001. Photosynthesis, photoinhibition, and nitrogen use efficiency in native and invasive tree ferns in Hawaii. *Oecologia* **126**: 345–354.

Ehrenfeld JG. 2003. Effects of exotic plant invasions on soil nutrient cycling processes. *Ecosystems* **6**: 503–523.

Ehrenfeld JG, Kourtev P, Huang WZ. 2001. Changes in soil functions following invasions of exotic understory plants in deciduous forests. *Ecological Applications* **11**: 1287–1300.

Gordon DR. 1998. Effects of invasive, non-indigenous plant species on ecosystem processes: lessons from Florida. *Ecological Applications* **8**: 975–989.

Gurevitch J, Hedges LV. 1993. Meta-analysis: Combining the results of independent experiments. In: Scheiner SM, Gurevitch J, eds. *Design and analysis of ecological experiments.* New York, NY, USA: Chapman & Hall. 378–389.

Gurevitch J, Hedges LV. 1999. Statistical issues in ecological meta-analyses. *Ecology* **80**: 1142–1149.

Harcombe PA, Cameron GN, Glumac EG. 1993. Above-ground net primary productivity in adjacent grassland and woodland on the coastal prairie of Texas, USA. *Journal of Vegetation Science* **4**: 521–530.

Hedges LV, Gurevitch J, Curtis PS. 1999. The meta-analysis of response ratios in experimental ecology. *Ecology* **80**: 1150–1156.

Hibbard KA, Archer S, Schimel DS, Valentine DW. 2001. Biogeochemical changes accompanying woody plant encroachment in a subtropical savanna. *Ecology* **82**: 1999–2011.

Hobbie SE. 1996. Temperature and plant species control over litter decomposition in Alaskan tundra. *Ecological Monographs* **66**: 503–522.

Hughes RF, Uowolo A. 2006. Impacts of *Falcataria moluccana* invasion on decomposition in Hawaiian lowland wet forests: The importance of stand-level controls. *Ecosystems* **9**: 977–991.

Jackson RB, Banner JL, Jobbagy EG, Pockman WT, Wall DH. 2002. Ecosystem carbon loss with woody plant invasion of grasslands. *Nature* **418**: 623–626.

Johnson NC, Wedin DA. 1997. Soil carbon, nutrients, and mycorrhizae during conversion of dry tropical forest to grassland. *Ecological Applications* **7**: 171–182.

Knops JMH, Bradley KL, Wedin DA. 2002. Mechanisms of plant species impacts on ecosystem nitrogen cycling. *Ecology Letters* **5**: 454–466.

Lett MS, Knapp AK, Briggs JM, Blair JM. 2004. Influence of shrub encroachment on aboveground net primary productivity and carbon and nitrogen pools in a mesic grassland. *Canadian Journal of Botany-Revue Canadienne de Botanique* **82**: 1363–1370.

Liang X, Zhang LQ, Zhao GQ. 2006. A comparison of photosynthetic characteristics between *Spartina alterniflora* and *Phragmites australis* under different CO_2 concentrations. *Acta Ecologica Sinica* **26**: 842–848.

Liao CZ. 2007. The effects of invasive alien plants on ecosystem carbon and nitrogen cycles. A case study of *Spartina alterniflora* invasion in the Yangtze estuary and a meta-analysis. *PhD Thesis*. Shanghai, China: Fudan University.

Luo YQ, Hui DF, Zhang DQ. 2006. Elevated CO_2 stimulates net accumulations of carbon and nitrogen in land ecosystems: a meta-analysis. *Ecology* **87**: 53–63.

Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M, Bazzaz FA. 2000. Biotic invasions: Causes, epidemiology, global consequences, and control. *Ecological Applications* **10**: 689–710.

Norris MD, Blair JM, Johnson LC. 2001. Land cover change in eastern Kansas: litter dynamics of closed-canopy eastern redcedar forests in tallgrass prairie. *Canadian Journal of Botany-Revue Canadienne de Botanique* **79**: 214–222.

Osenberg CW, Sarnelle O, Cooper SD, Holt RD. 1999. Resolving ecological questions through meta-analysis: goals, metrics, and models. *Ecology* **80**: 1105–1117.

Pastor J, Aber JD, McClaugherty CA, Melillo JM. 1984. Above-ground production and N and P cycling along a nitrogen mineralization gradient on blackhawk island, Wisconsin. *Ecology* **65**: 256–268.

Pimentel D, Lach L, Zuniga R, Morrison D. 2000. Environmental and economic costs of nonindigenous species in the United States. *Bioscience* **50**: 53–65.

Richter DD, Markewitz D, Trumbore SE, Wells CG. 1999. Rapid accumulation and turnover of soil carbon in a re-establishing forest. *Nature* **400**: 56–58.

Rothstein DE, Vitousek PM, Simmons BL. 2004. An exotic tree alters decomposition and nutrient cycling in a Hawaiian montane forest. *Ecosystems* **7**: 805–814.

Svejcar T, Sheley R. 2001. Nitrogen dynamics in perennial- and annual-dominated arid rangeland. *Journal of Arid Environments* **47**: 33–46.

Vitousek PM. 2004. *Nutrient cycling and limitation: Hawaii as a model system.* Princeton, NJ, USA: Princeton University Press.

Vitousek PM, Dantonio CM, Loope LL, Rejmanek M, Westbrooks R. 1997. Introduced species: a significant component of human-caused global change. *New Zealand Journal of Ecology* **21**: 1–16.

Vitousek PM, Howarth RW. 1991. Nitrogen limitation on land and in the sea: How can it occur? *Biogeochemistry* **13**: 87–115.

Vitousek PM, Walker LR. 1989. Biological invasion by *Myrica faya*. Hawaii – plant demography, nitrogen-fixation, ecosystem effects. *Ecological Monographs* **59**: 247–265.

Weber E, Li B. in press. Plant invasions in China: what is to be expected in the wake of economic development? *Bioscience*.

Wilsey BJ, Polley HW. 2006. Aboveground productivity and root-shoot allocation differ between native and introduced grass species. *Oecologia* **150**: 300–309.

Windham L, Ehrenfeld JG. 2003. Net impact of a plant invasion on nitrogen-cycling processes within a brackish tidal marsh. *Ecological Applications* **13**: 883–896.

Windham L, Weis JS, Weis P. 2004. Metal dynamics of plant litter of *Spartina alterniflora* and *Phragmites australis* in metal-contaminated salt marshes. Part 1: patterns of decomposition and metal uptake. *Environmental Toxicology and Chemistry* **23**: 1520–1528.

Witkowski ETF. 1991. Effects of invasive alien acacias on nutrient cycling in the coastal lowlands of the cape fynbos. *Journal of Applied Ecology* **28**: 1–15.

Supplementary Material

The following supplementary material is available for this article online:

Text S1 A list of 94 papers from which the data were extracted for this metadata analysis

Figs S1 and S2 Two figures of frequency distribution of logarithm of response ratio (RR) of 14 variables ($n > 30$) related to C and N cycles under plant invasion.

Table S1 Weighted response ratio (RR_{++}) and number of data sets (in parentheses) of 20 variables extracted from each of the papers

Table S2 A table of 95% confidence intervals of weighted response ratio (RR_{++}) and sample size (n) of 20 variables related to C and N cycles under the invasions of woody and herbaceous species and of N-fixing and nonN-fixing species, and in forests, grasslands and wetlands

This material is available as part of the online article from: http://www.blackwell-synergy.com/doi/abs/10.1111/j.1469-8137.2007.02290.x
(This link will take you to the article abstract).