Altered ecosystem carbon and nitrogen cycles by plant invasion:

A meta-analysis

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Summary

• Plant invasion potentially alters ecosystem carbon and nitrogen cycles. However, the overall direction and magnitude of such alteration are poorly quantified.

• We synthesized 94 experimental studies, using a meta-analysis approach, to quantify the changes of 20 variables associated with carbon and nitrogen 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 7% increase in soil carbon stock to a 133% increase in shoot carbon stock. Flux variables, such as aboveground net primary production and litter decomposition increased by 50 - 120% in invaded ecosystems, compared to native ones. Plant nitrogen concentration, soil $\text{NH}_4^+$ and $\text{NO}_3^-$ concentrations were 40%, 30% and 17% higher in invaded than native ecosystems, respectively. Increases in plant production and soil nitrogen availability indicate that there were positive feedbacks between plant invasion and carbon and nitrogen cycles in invaded ecosystems.

• Invasions by woody and N-fixing plants tended to have greater impacts on carbon and nitrogen cycles than those by herbaceous and non-N-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 due to the expansion of global trade, agriculture and many other human activities (Vitousek et al., 1997; Mack et al., 2000; Weber & Li, 2006). 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, we urgently 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 (e.g., 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 native ecosystems (e.g., 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 feedbacks 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 an 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 aboveground litter of the invasive *Phragmites australis* decomposed more slowly than 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 vimineum* 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 non-N-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 non-N-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 two years 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) have reviewed the studies of M. faya invasion in Hawaii
Volcanoes National Park, and Gordon (1998) has 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) has 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 can not
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, we synthesized 94 experimental studies, 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, we used
the meta-analysis 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, were there any positive
feedbacks between plant invasion and C and N cycles in invaded ecosystems?
Methods

Data sources

To avoid bias in publication selection, we set the following five criteria for the inclusion of data related to C and N cycles with reference to plant invasion. 1) The invasive species examined were vascular higher plants. 2) The ecosystems contained both invasive and native plant species. 3) The studies directly compared invaded ecosystems dominated by invasive species with the corresponding native ones in terms of C and N cycles. 4) 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). 5) Where experiments involved reciprocal transfers of invasive and native species, we only collected data of invasive species in invaded ecosystems and native species in native ecosystems.

We collected data from 94 published experimental studies (see Appendix A). In total, 20 variables associated with C and N cycles were examined in invaded and native ecosystems (see Appendix B). Pool variables included C and N stocks in shoots, roots, litter, soils and soil microbes. Flux variables included aboveground 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 belowground 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, we extracted the mean ($M$), standard error ($SE$) or standard deviation ($SD$) or confidence interval ($CI$), and sample size ($n$) in both invaded and native ecosystems. 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. We did not distinguish soil organic C stock 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 ($\bar{M}$) and the averaged standard error ($\bar{SE}$) of the variable were estimated as:

$$\bar{M} = \frac{\sum M_j}{j}$$  \hspace{1cm} (1)$$

$$\bar{SE} = \sqrt{\frac{\sum SE_j^2(n_i-1)n_i}{\left(\sum n_i - 1\right)\sum n_i}}$$  \hspace{1cm} (2)$$

where $j$ is the sampling times ($\geq 2$), $M_j$, $SE_j$ and $n_i$ were mean value, standard error and sample size on the $i$th sampling date, respectively.

The constructed database consisted of 1,045 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 including both symbiotic and associative fixers, e.g., *Prosopsis*, *Acacia*, *Myrica* and *Spartina* and non-N-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 \( RR \) 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 

\[
\left(e^{RR_{++}} - 1\right) \times 100\%
\]

If the 95% CIs of \( RR_{++} \) for a variable did not overlap between the invasive woody and herbaceous species, between the invasive N-fixing and non-N-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 type of ecosystems. If the 95% CIs of \( RR_{++} \) overlapped, student t-test was used to further examine whether or not the difference was significant between or among them.

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

\[
y = ae^{-\frac{(x-\mu)^2}{2\sigma^2}}
\]  

(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 \( x = \mu \), \( \mu \) and \( \sigma^2 \) 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 1-2 in Appendix C), and the 14 $\mu$ values from the model of Gaussian function were all consistent with the corresponding $RR_{++}$ (Figs 1-2 in Appendix C 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 native ecosystems, respectively (Table 1). In invaded ecosystems, for C pools, the percentages of increases in both roots and soils were lower than those in shoots, litter and soil microbes (all $P < 0.001$). For N pools, the percentages of increases in plants were higher than those in soils and soil microbes in invaded ecosystems (all $P < 0.001$).

Aboveground net primary production (ANPP), 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 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 herbaceous ones, respectively (all $P < 0.05$) (Fig. 2a and Appendix D). The rest of $RR_{++}$ 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 non-N-fixing ones, respectively (Fig. 2b; Appendix D). For most of the 20 variables, invasions of both herbaceous and non-N-fixing plants had also significant impacts on C and N cycles in invaded ecosystems, compared to native ecosystems (Fig. 2a, b; Appendix D). Forests, grasslands, and wetlands all responded significantly to plant invasion in relation to C and N cycles, and their responses were similar (Fig. 2c and Appendix D).
Discussion

Methodological considerations

As in most similar studies, the published studies used in this study might 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 due to the lack of sufficient published data. The data sets collected in our study might have come from regions where ecologists have conducted studies on the invasion for many years, for example, on the Hawai’ian islands (Vitousek & Walker, 1989; Baruch & Goldstein, 1999; Hughes & Uowolo, 2006; etc.), while many other invaded regions have not attracted such an attention from ecologists. This may cause uncertainties in evaluation of 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 less 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 dataset 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 due to 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 to 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 to 80 days longer than that of the native P. australis and Scirpus maritimer 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 (e.g., 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...
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 native ones. As with ANPP, the increases in soil N mineralization and nitrification could arise from ecophysiological differences between native and invasive species (e.g., 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 of 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.

N 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 ecosystems (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 ten 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 due to 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 ecosystems.

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 native ecosystems (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 and Appendix C Figs. 1-2). This variability reflects diverse responses of various C and N processes to the invasion of a given species, and points to the need of 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 non-N-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 the invasive woody than herbaceous species, and for invasive N-fixing than non-N-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 non-N-fixing plants. Thus, any differential effects due to the differences in ecophysiological traits between invasive woody and herbaceous species, invasive N-fixing and non-fixing 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 $\text{NH}_4^+$ and $\text{NO}_3^-$ concentrations across invasive woody and herbaceous species, invasive N-fixing and non-N-fixing plants, and in forests, grasslands and wetlands (Fig. 2 and Appendix D). 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 we did not find sufficient experimental data to examine the impacts of plant invasion on rates of N fixation (three cases) and loss (no data available). The increased $\text{NH}_4^+$ and $\text{NO}_3^-$ 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 aspect, it is different from the opinion that plant invasion has detrimental effects on ecosystems (e.g., 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 functions 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 macro-elements. 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 showed 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 accelerated 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 non-N-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.

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References


Table 1 Percentage of change of 20 variables related to C and N cycles in response to plant invasion.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Percentage of change $(e^{RR} - 1) \times 100%$</th>
<th>$n$</th>
<th>Variable</th>
<th>Percentage of change $(e^{RR} - 1) \times 100%$</th>
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<tbody>
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<td>Fluxes</td>
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<tr>
<td>Shoots</td>
<td>132.71 ± 2.38</td>
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<td>ANPP</td>
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<td>Roots</td>
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<td>LIDE</td>
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<td>Litter</td>
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<td>SNNM</td>
<td>51.80 ± 6.91</td>
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<tr>
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<td></td>
<td>SNHC</td>
<td>29.68 ± 2.98</td>
<td>87</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>SNOC</td>
<td>16.58 ± 3.47</td>
<td>77</td>
</tr>
</tbody>
</table>

Note: Percentage of change represents as the mean ± 95% confidence intervals. Abbreviations:

ANPP-aboveground 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.
Figure legends

Fig. 1 Weighted response ratio ($RR_{++,}$) of 20 variables related to C and N cycles in response to plant invasion. Bars represent $RR_{++,}$ ± 95% confidence intervals. See Table 1 for the abbreviations of variables. The vertical line was drawn at $RR = 0$

Fig. 2 Weighted response ratios ($RR_{++,}$) of 20 variables related to C and N 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. See Table 1 for the abbreviations of variables. The vertical lines were drawn at $RR = 0$. See Appendix D for details

Fig. 3 Potential positive feedbacks between plant invasion and C and N cycles in invaded ecosystems.

Note: ↑- positive response to plant invasion. ?- not clear for the response to plant invasion
Weighted response ratio ($RR_{++}$)

-0.8 -0.4 0.0 0.4 0.8 1.2

Carbon pools
- Shoots
- Roots
- Litter
- Soils
- Microbe

Nitrogen pools
- Shoots
- Roots
- Soils
- Microbe

Fluxes
- ANPP
- LIDE
- SNNM
- SNNN
- PNCO
- LNCO
- LLCO
- LCNR
- LLNR
- SNHC
- SNOC

Fig. 1
a) Life forms
- Shoots
- Roots
- Litter
- Soils
- Microbe

b) Functional groups of N fixation
- N-fixing
- Non-N-fixing

c) Ecosystem types
- Forests
- Grasslands
- Wetlands

Fig. 2
Plant invasion

Plant biomass
↑ 5-132% C stock
↑ 86-112% N stock

Soil microbial biomass
↑ 34% C stock
↑ 26% N stock

Litter biomass
↑ 49% C stock
↑ 38% N concentration

Soil organic matter
↑ 7% C stock
↑ 18% N stock

↑ 53% Nitrification

↑ 30% NH₄⁺

↑ 17% NO₃⁻

↑ 83% NPP

↑ 117% Litter decomposition

↑ 52% Net N mineralization

↑ 53% Nitrification

↑ 17% NO₃⁻

↑ 86-112% N stock
Appendix A

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

Appendix B

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

Appendix C

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

Appendix D

A Table of 95% CIs 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 non-N-fixing species, and in forests, grasslands and wetlands