



Can ecological stoichiometry help explain patterns of biological invasions?

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Several mechanisms for biological invasions have been proposed, yet to date there is no common framework that can broadly explain patterns of invasion success among ecosystems with different resource availabilities. Ecological stoichiometry (ES) is the study of the balance of energy and elements in ecological interactions. This framework uses a multi-nutrient approach to mass-balance models, linking the biochemical composition of organisms to their growth and reproduction, which consequently influences ecosystem structure and functioning. We proposed a conceptual model that integrates hypotheses of biological invasions within a framework structured by fundamental principles of ES. We then performed meta-analyses to compare the growth and production performances of native and invasive organisms under low- and high-nutrient conditions in terrestrial and aquatic ecosystems. Growth and production rates of invasive organisms (plants and invertebrates) under both low- and high-nutrient availability were generally larger than those of natives. Nevertheless, native plants outperformed invasives in aquatic ecosystems under low-nutrient conditions. We suggest several distinct stoichiometry-based mechanisms to explain invasion success in low- versus high-nutrient conditions: higher resource-use efficiency (RUE; C:nutrient ratios), threshold elemental ratios (TERs), and trait plasticity (e.g. ability of an organism to change its nutrient requirements in response to varying nutrient environmental supply); high-nutrient conditions: higher growth rates and reproductive output related to lower tissue C:nutrient ratios, and increased trait plasticity. Interactions of mechanisms may also yield synergistic effects, whereby nutrient enrichment and enemy release have a disproportionate effect on invasion success. To that end, ES provides a framework that can help explain how chemical elements and energy constrain key physiological and ecological processes, which can ultimately determine the success of invasive organisms.

Biological invasions represent one of the major drivers of environmental change and a strong threat to biodiversity and ecosystem functioning worldwide (Vitousek et al. 1997, Sala et al. 2000, Davis 2003, Hooper et al. 2005). The establishment and spread of an invasive self-sustaining population outside its native range is a function of both abiotic and biotic factors, such as invasive propagule pressure, the abiotic characteristics of the invaded ecosystem, the traits of the invaders, as well as ecological interactions between the invasive population and the native community (Richardson et al. 2000, Keane and Crawley 2002, Richardson and Pyšek 2006, Catford et al. 2009). As only a small fraction of all introduced organisms become invasive (Richardson and Pyšek 2006), understanding why and how some introduced plants and animals become successful invaders is paramount to maintaining native community biodiversity and ecosystem functioning (Srivastava and Vellend 2005).

Considerable research has attempted to uncover mechanisms explaining success of invasive organisms across ecosystems with different resource availabilities. For example, the ‘fluctuating resource availability theory’ directly links resource availability and community invasibility, stating that short-term inputs of resources (usually associated with anthropogenic or ‘natural’ disturbances) facilitate colonization by relaxing resource limitation (Davis et al. 2000). However, as both native and exotic organisms may equally profit from higher resource availability, this theory is insufficient to explain why invasive organisms outperform natives (Blumenthal et al. 2009). Another intuitively appealing hypothesis for the rapid establishment and success of invasive organisms is the ‘enemy release hypothesis’, which suggests that exotic organisms succeed due to the scarcity of natural enemies (e.g. predators or pathogens) in their introduced compared to their native range (Keane and Crawley 2002). Recent evidence

also suggests that enemy release might positively interact with resource availability to explain invasion success ('resource-enemy release hypothesis'; Blumenthal 2005, 2006, Blumenthal et al. 2009). Plants adapted to high-resource levels in their native range are often particularly susceptible to enemies, as they are fast growing, highly nutritious, and generally poorly defended (low investment in chemical and structural defenses). These 'high-nutrient' organisms may therefore benefit most from having fewer enemies in their introduced range (Blumenthal 2006, Blumenthal et al. 2009).

Nutrient-rich habitats often experience more invasions than nutrient-poor habitats. However, invasions can also occur in low-resource ecosystems (Burns 2006, Funk and Vitousek 2007, Young and Mangold 2008). Invasive organisms may succeed in these environments by displaying resource conservation traits such as higher resource use efficiency (RUE; higher C:nutrient ratios, *sensu* Vitousek 1982). Further, 'resource competition theory' (Tilman 1982) predicts that the probability of establishment of an invasive organism increases if the invader has lower requirements for resources (R^*) to sustain higher growth rates and reproductive outputs than those of natives when resources are limiting (Shea and Cheeson 2002, Stachowicz and Tilman 2005). Finally, it has been suggested that adaptive plasticity in life history traits and rapid evolutionary change are also important mechanisms explaining invasiveness, as both enable introduced organisms to cope with the environmental barriers of the invaded habitat (Rejmánek and Richardson 1996, Claridge and Franklin 2002, Prentis et al. 2008, Whitney and Gabler 2008). Indeed, trait plasticity allows invaders to allocate more nutrients to reproductive biomass than their native counterparts (Drenovsky et al. 2008, Funk 2008).

Consequently, ecosystem resource availability, organism nutrient requirements, and individual competitiveness for resources may be the main interacting mechanisms explaining success of invasive organisms, because higher resource uptake, growth, and reproduction are necessary to enable organisms to successfully spread into new habitats (Daehler 2003, Richardson and Pyšek 2006). Therefore, understanding invasion success in low- and high-resource environments requires an integration of traits from the invasive organisms as well as the invaded ecosystem (Vitousek 1982, Funk and Vitousek 2007, Drenovsky et al. 2008).

Ecological stoichiometry framework: a multi-nutrient approach

Ecological stoichiometry theory focuses on understanding how the structure and functioning of biological systems both influence and are influenced by the balance of chemical elements and energy (carbon:nitrogen:phosphorus [C:N:P] ratios) between organisms and their environment (Elser et al. 2000a, Sterner and Elser 2002). In general, the conceptual development of ES has focused on individual-level responses to resource stoichiometry (e.g. growth rates; Elser et al. 2003), population dynamics (Anderson et al. 2004), competitive interactions (Yoshida 2006), and the structure and functioning of ecosystems (Elser and Urabe 1999, Sterner and Elser 2002). Organisms with high growth rates and reproductive outputs (i.e. higher fitness) have high nutrient demands (lower tissue C:nutrient ratios, especially lower

N:P ratios; Sterner and Elser 2002) and potentially have a competitive advantage in high-P environments. Therefore, there are different competitive abilities among plants and among animals for nutrients, based on their tissue nutrient content and life history traits (Tilman 1982, Sterner and Elser 2002, Karasov and Martínez del Río 2007). Here, we concentrate on the generality of consumer-resource stoichiometry as it relates to competitive interactions of plants and animals under low- and high-resource availabilities.

Intra- and interspecific variation in plant nutrient content reflects differences in nutrient supply, plant traits and physiological mechanisms that determine how efficiently the nutrients are used for growth (Sterner and Elser 2002, Güsewell 2004, Ågren 2008). A key implication here is that primary producers may change their elemental content as an adaptive response to differential nutrient availability (Ventura et al. 2008). Under low-nutrient conditions, growth is slow, biomass C:nutrient ratios increase, and plants use nutrients more efficiently (Vitousek 1982). In contrast, under high-nutrient conditions, plants maximize protein synthesis and growth as competitive strategies (Vitousek 1982, Matzek and Vitousek 2009), resulting in decreased tissue C:nutrient ratios (Ågren 2008). Nevertheless, not all plants change their C:N:P stoichiometry in response to nutrient availability in the same way, and differences in N:P optimal ratios play a key role for nutrient competition among autotrophs (Tilman 1982, Sterner and Elser 2002).

Although the tissue C:N:P ratios of autotrophs are widely variable, the elemental composition of animals is relatively fixed and is mainly driven by differences in their growth rates (Elser et al. 1996, Sterner and Elser 2002). The mechanistic link between consumer body stoichiometry and growth rate has been proposed in the 'growth rate hypothesis' (GRH; Elser et al. 2003). This hypothesis states that variation in organism C:N:P stoichiometry (especially body C:P and N:P ratios) is linked to increased body P content in order to meet the demands of higher growth rates and/or reproduction (Elser et al. 2003). Such stoichiometric differences between plants and animals have major implications for the structure and functioning of biological systems (Sterner and Elser 2002, Moe et al. 2005). As animals usually require chemical elements in different ratios than those provided by their food resources, their growth and reproduction is constrained by resource limitation (Sterner and Elser 2002, Anderson et al. 2004, Moe et al. 2005). Further, ES models predict a tradeoff between maximal growth rates and the likelihood of P-limitation, thus, fast-growing animals may be more severely constrained by P availability, and in turn should be less competitive when resource C:P ratios are high (Sterner and Elser 2002, Elser et al. 2000a).

A key approach for understanding nutrient or energy limitation in consumers is the threshold elemental ratio (TER), the critical C:nutrient ratio above which a nutrient is limiting for growth (Frost 2005). TER is predicted to be a function of consumer physiological requirements for nutrients as well as food quantity (Urabe and Watanabe 1992, Anderson and Hessen 2005, Frost et al. 2006). Carbon:nutrient TERs are predicted to vary across taxa revealing differences in their metabolic demands for growth and maintenance (Frost et al. 2006). Energy and nutrient availability therefore sets optimal constraints on resource allocation strategies to all

fitness-related processes (Brown et al. 2004). For example, fast-growing animals have relatively low C:P-TERs, and have higher fitness (i.e. faster growth and reproduction) in P-rich environments, but might suffer strong growth penalties in P-poor environments (Sternler and Elser 2002, Frost et al. 2006). In contrast, consumers with high C:P-TERs (high C:P ratios), allowing them to succeed in P-poor environments (Frost et al. 2006). Therefore, differences in consumer growth under variable resource C:N:P stoichiometry are useful to understand how energy and nutrient availability can constrain consumer growth influencing its population growth and competitive interactions.

Despite increasing use of stoichiometric rules to answer diverse ecological questions, ES has rarely been used to explain the success of invasive organisms (but see Acharya et al. 2006, Naddafi et al. 2009, Smith et al. 2009, Wang et al. 2009). As the elemental requirements of all organisms adhere to the law of conservation of mass (Sternler and Elser 2002, Karasov and Martínez del Río 2007), the general principles of ES should apply to both invasive and native organisms and may thus provide added insight into understanding the proliferation of invasive organisms across ecosystems with different nutrient availabilities.

Linking invasion biology to ecological stoichiometry

Our main objective is to provide a basis for testing mechanistic hypotheses of biological invasions under the framework of ES. Here, we couple a conceptual model with meta-analyses to: 1) propose stoichiometric-based mechanisms that could broadly help explain invasion success under low- and high-nutrient availabilities, and 2) compare the growth and production performances of native and invasive organisms under low-nutrient conditions and under experimental nutrient enrichment in terrestrial and aquatic ecosystems, assuming that higher performances of invasive organisms as compared to natives should be associated with invasion success.

The conceptual model

Our proposed conceptual model integrates previous hypotheses of biological invasions within a formal framework based on stoichiometric principles. Specifically, we expand and integrate core aspects of the 'fluctuating resource availability theory' (Davis et al. 2000, Davis and Pelsor 2001), the 'resource competition theory' (Tilman 1982), the 'resource-enemy release hypothesis' (Blumenthal et al. 2009), the 'growth rate hypothesis' (GRH; Elser et al. 2003) and adaptive plasticity (Richards et al. 2006, Funk 2008) to help explain patterns of invasion success across ecosystems (Fig. 1).

I. Low-nutrient environments

To outperform native organisms in a low-resource environment, invasive organisms must be more efficient at acquiring and using limited resources (Funk and Vitousek 2007). We propose that both invasive plants and animals have higher tissue C:nutrient ratios (Funk and Vitousek 2007, Martin et al. 2009, Naddafi et al. 2009) and also that invasive animals have higher C:nutrient-TERs (Naddafi et al. 2009, Smith et al. 2009, Wang et al. 2009), resulting in lower

nutrient requirements, and also less growth limitation under nutrient-poor conditions. In addition, we suggest that invasive organisms that succeed in low-nutrient environments have lower nutrient requirements for growth and reproduction than natives (lower R*; Tilman 1982, Shea and Cheeson 2002). For example, we predict that under N-limitation, invasive organisms having higher tissue C:N ratios and high C:N-TER will outcompete natives with higher requirements for N (low tissue C:N and C:N-TERs). The equivalent pattern is expected under P-limitation.

We also suggest that invasive organisms can achieve higher growth rates and reproductive outputs than natives in low-nutrient environments if they display higher trait plasticity (Funk 2008, Naddafi et al. 2009). Current knowledge has shown that adaptive changes in stoichiometric traits, such as varying tissue nutrient content and growth rates confer an adaptive advantage (Jeyasingh and Weider 2005, 2007, Jeyasingh et al. 2009). Moreover, organisms with a greater competitive advantage in nutrient-poor environments are those able to modify their body nutrient content and increase efficiency of nutrient use without major decreases in their growth rates and/or reproduction outputs (Elser et al. 2003, Mulder and Bowden 2007). Thus, adaptive changes might lead to increased invasion success under nutrient-limited conditions (Funk 2008, Naddafi et al. 2009). Finally, invasive organisms that are able to actively increase resource availability, in particular through N₂-fixation, outperform natives in low-nitrogen environments.

II. High-nutrient environments

According to the GRH (Elser et al. 2003), organisms with high-nutrient content (low C:nutrient ratios, especially low C:P and N:P ratios) commonly have higher growth rates (higher development and reproductive outputs). Indeed, differences in growth rates between native and invasive organisms are thought to be a major factor determining invasiveness, allowing invasives to exploit available resources more efficiently than slow-growing native organisms (James and Drenovsky 2007). We therefore hypothesize that invasive organisms will outcompete natives under nutrient-rich conditions if they have lower tissue C:nutrient ratios (and lower tissue N:P ratios) associated with higher growth rates and reproductive outputs. We also suggest that plasticity in organismal traits (e.g. reproduction) facilitate invasion success in nutrient-rich environments (Burns 2006). However, the magnitude of the plastic responses displayed by invasive organisms is thought to be greater when nutrient availability is low and lower when nutrients are in high supply (Aikio and Markkola 2002). This implies that evolutionary processes that directly or indirectly generate variation in major life history traits can have strong consequences for ecological dynamics, such as competitive interactions (Elser et al. 2000b).

III. Enemy release–resource synergistic interaction

Additionally, the model proposes a synergistic interaction between nutrient availability, enemy release, and resource allocation that may ultimately explain invasion success among plants and animals. Invasive organisms may be released from their enemies in the invaded range (Schierenbeck et al. 1994, Mitchell and Power 2003, Torchin and Mitchell 2004, Blumenthal et al. 2009, Seastedt 2009) and this effect can be stronger for organisms that are adapted to high-resource levels

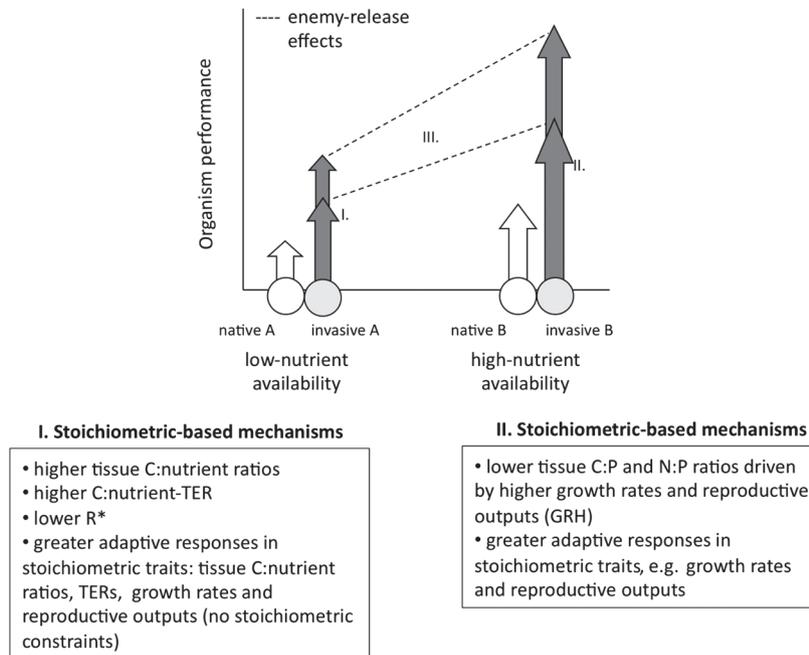


Figure 1. Conceptual model of different stoichiometric mechanisms displayed by invasive organisms (producers and consumers) to outperform native organisms in low- and high-nutrient environments. In the model, we propose that invasive organisms (A and B) have higher performance (growth rates and/or reproduction) than natives (A and B) due to either one of the following stoichiometric mechanisms: (I) higher tissue C:nutrient ratios (higher nutrient use efficiency, NUE), higher threshold elemental ratios (TER) under low nutrients, lower nutrient requirements for growth and reproduction than natives (lower R^*) and greater trait plasticity (e.g. greater adaptive changes in body nutrient content). Although not explicitly indicated in the conceptual model, nitrogen-fixing plants (invasive and native) have lower tissue C:N (higher N:P ratios), and therefore their invasion success is not constrained by N. (II) Lower tissue C:nutrient ratios driven by higher growth rates and reproductive outputs ('growth rate hypothesis'), and greater adaptive changes in stoichiometric traits. (III) A synergistic interaction between nutrient availability, enemy release, and resource allocation (illustrated by the dashed lines, a higher performance of invasives driven by the synergistic interaction). Enemy-release effects can be stronger for organisms that are adapted to high-resource levels in their native range (right side of the figure), as they are fast-growing, have low tissue C:nutrient ratios, and are generally poorly defended. Enemy release might also be important for invasive success of 'low-resource organisms', as these often well-defended invasive organisms may evolve lower resource allocation to defense and more resources to growth and reproduction (left side of the figure).

For simplicity, the performance of native and invasive organisms is illustrated by a single response (e.g. growth rate) and the height of the arrows indicates the response magnitude. Further, we implicitly include a single resource (N or P) in the model, but depending on whether N or P is limiting, performances could vary in relation to nutrient requirements of the invasive organism.

in their native range, as they are fast-growing, highly nutritious (low tissue C:nutrient ratios), and often poorly defended due to low investment in chemical and structural defenses (i.e. 'resource–enemy release hypothesis'; Blumenthal 2005, 2006, Frost et al. 2008, Blumenthal et al. 2009). However, enemy release might also be important for invasive success of 'low-resource organisms', as these invaders may evolve lower resource allocation to defense (particularly defense against specialist enemies), and more resource allocation to growth and reproduction ('evolution of increased competitive ability hypothesis'; Blossey and Notzold 1995, Agrawal 2001, Blumenthal 2006).

Meta-analyses comparing the performance of invasive and native organisms under low- and high-nutrient conditions

We performed two separate meta-analyses (meta-analysis I: invasive and native organisms under low nutrient conditions; meta-analysis II: invasive and native organisms under experimental nutrient enrichment) to compare the performance of invasive and native organisms in different nutrient conditions and ecosystems (i.e. terrestrial vs aquatic; temperate grasslands vs tropical forests vs agro-ecosystems). Based on

our model predictions, we hypothesized that invasive organisms are able to outperform natives in both low- (model prediction I and III) and high-nutrient environments (model prediction II and III). Nevertheless, because we did not find enough data for testing model prediction III, we only discuss synergistic interactions of the 'resource–enemy release hypothesis' with other mechanisms for increasing invasion success. We also expected that differences in performance of invasive and native organisms depend on nutrient identity (N or P) and ecosystem type. Some existing paradigms identify N as the primary limiting nutrient in terrestrial ecosystems (Vitousek and Howarth 1991) and P as the main limiting nutrient in aquatic ecosystems (Schindler 1977), although recent work indicates that N and P limitations are equivalent in terrestrial and aquatic ecosystems (Elser et al. 2007). Terrestrial organisms from tropical and temperate ecosystems are also likely to vary in their response to N and P. Tropical ecosystems not disturbed by glaciation are thought to be more frequently limited by P because of greater soil age, whereas temperate ecosystems may be more often limited by N (Reich and Oleksyn 2004). Finally, differences in consumer specialization between aquatic and terrestrial ecosystems can generate differences in invasion success across

ecosystems (Parker and Hay 2005). Many aquatic herbivores are trophic generalists with a low degree of diet specialization, whereas many terrestrial herbivores are specialists (Shurin et al. 2006). Introduced plants in aquatic ecosystems might therefore not escape consumption if generalist herbivores functionally replace their native enemies. In contrast, stronger enemy-release effects are expected from specialist terrestrial herbivores (Keane and Crawley 2002, Vermeij et al. 2009).

Methods

Study selection and data criteria

We searched the ISI Web of Science database (1980–2009) by using combinations of key words, such as invasive, invader, naturalized, non-native, nitrogen, phosphorus and nutrient. We also searched in the reference lists of papers identified by this search. We selected studies that reported environmental nutrient availability (N content, P content, C:N, C:P and N:P ratios). We focused on N and P because these elements are considered key limiting nutrients for primary production and plant–animal interactions (Vitousek 2004). Performance indicators of invasive and native organisms (plants and animals) in terrestrial and aquatic (freshwater, marine) ecosystems included: production, growth rate, and reproductive output. We included studies containing proxy data for production (i.e. biomass, density and percent cover).

Studies were omitted if they did not include data on response variables of invasive and/or native organisms, treatments were not replicated, and if observations were not independent. Studies were included if they met the following criteria: (1) reported means and standard errors, standard deviations or confidence intervals, sample sizes, correlation and/or regression estimates, and *p*-values for response and treatment variables, (2) were controlled and manipulative studies, and (3) contained at least one native and invasive organism from one or more ecosystem type. For studies including multiple native and/or invasive organisms, we considered each data point as independent (Gurevitch et al. 1992). We considered multiple results within the same study as independent when they reported multiple response variables for one organism or multiple organisms for one response variable. Data containing multiple treatments and responses over time were averaged. When statistical data were presented in figures, we used GraphClick (Arizona Software Inc., USA) to extract the data. Our final dataset included a total of 382 cases of 176 native and 206 invasive organisms, 203 for producers and 179 for consumers (herbivores and detritivores) from 46 papers (Supplementary material Appendix 1).

Data analysis

Two separate meta-analyses (meta-analysis I: invasive and native organisms under low-nutrient conditions; meta-analysis II: invasive and native organisms under experimental nutrient enrichment) were performed using the MetaWin 2.0 software (Rosenberg et al. 2000). Effect sizes were estimated using Hedges' *d*: the difference between the values of control and treatment divided by a pooled standard deviation and weighted by sample size (Rosenberg et al. 2000).

In meta-analysis I, we estimated the effect sizes between the performance (production, growth and reproduction) of native and invasive organisms under low-nutrient conditions (defined as 'control' in the original studies) as the mean difference between native and invasive organism performance responses. A significant positive effect size indicates that the performance is higher for invasive organisms than natives, and a significant negative effect size indicates that the performance is higher for native than invasive organisms. If the low-nutrient condition was reported as an increase in C:N or C:P ratios, the data were treated as in Meta-analysis II.

In meta-analysis II, we estimated the effect sizes between the performance of native and invasive organisms under experimental nutrient enrichment as the mean difference between low- (control) and high-nutrient availability (treatment). Then, we compared the effect sizes between invasive and native organisms among and within ecosystems. For both meta-analyses we categorized data by taxonomic group (plants and invertebrates), ecosystem type (terrestrial and aquatic) and nutrient identity (N, P or N:P ratios). The terrestrial ecosystems were further divided into tropical forests, temperate grasslands, and agricultural ecosystems. Data from studies in wetland ecosystems were categorized as aquatic.

We used bias-corrected bootstrapped 95% confidence intervals (CIs) to determine if effect sizes differed significantly from zero (i.e. the treatment and control were significantly different from each other). A negative effect size indicates a lower performance of invasive in comparison to native organisms (meta-analysis I), or a decrease in the performance of invasive and native organisms under increased nutrient availability (meta-analysis II). Student's *t*-tests were performed to examine the difference in effect sizes for invasive organisms responses between ecosystem types and between invasive and native organism performance.

As the file drawer problem introduces bias to meta-analysis (Gurevitch and Hedges 1999, Rosenberg et al. 2000), we used two different metrics to estimate potential publication bias. We examined a funnel plot of effect size estimates and sample sizes, according to common interpretations, with symmetrical plots indicating non-bias. In addition, we used the fail-safe number to estimate whether publication biases (if they exist) could be safely ignored (Rosenberg 2005). Results from the fail-safe numbers were high enough to be confident of the robustness of our results against publication bias (Rosenberg 2005).

We tested for homogeneity among effect sizes using a *Q* test, and these values were tested using χ^2 (significance level $p < 0.05$) (Rosenberg et al. 2000). Because our data showed heterogeneity in effect sizes we performed a meta-analysis considering comparisons across main categories and, if enough data were available, within fine-grained categories (e.g. terrestrial; temperate vs tropical, grassland vs forest). We were unable to perform all comparisons within categories because 1) most of the original studies focused on nitrogen effects and very few included resource C:N or N:P ratios, 2) few studies reported performances of native and invasive aquatic invertebrates, 3) most studies were performed in ecosystems located in the northern hemisphere, and 4) tropical ecosystems were under-represented in invasive plant studies. All results show the mean weighted effect size and 95% bootstrapped CIs (Rosenberg et al. 2000).

Results

Meta-analysis I: invasive and native organisms under low-nutrient conditions

Plant invasions

Invasive and native plant performances under low-nutrient levels varied among ecosystem types and according to nutrient identity (N or P). Under low-N conditions, we found higher production for invasive than native plants in terrestrial ecosystems, whereas native plants outperformed invasives in aquatic ecosystems (Fig. 2). The differences between ecosystems were significant (t -test: -4.13 , $p < 0.001$). No significant differences in the performance of aquatic invasive plants and natives were found under low-P conditions [-0.26 (-2.05 to 0.48)]. Note that, due to a lack of suitable studies, the response of terrestrial plants to low-P conditions could not be analyzed.

Invertebrate invasions

Production responses to increases in food C:N or C:P ratios (i.e. low P or N food quality) were not significantly different from zero for either invasive or native invertebrates (Table 1A). Invasive invertebrates responded more strongly than natives to increased C:P ratios, but responses to increased C:N ratios were similar. Invasive reproduction showed a significant negative response to increased food C:P ratios. Note that, due to a lack of suitable studies, the response of invertebrates to low-nutrient conditions was analyzed by pooling the data from aquatic and terrestrial studies.

Meta-analysis II: invasive and native organisms under experimental nutrient enrichment

Plant invasions

For both terrestrial and aquatic ecosystems, invasive plants generally showed a higher performance (growth and/or production)

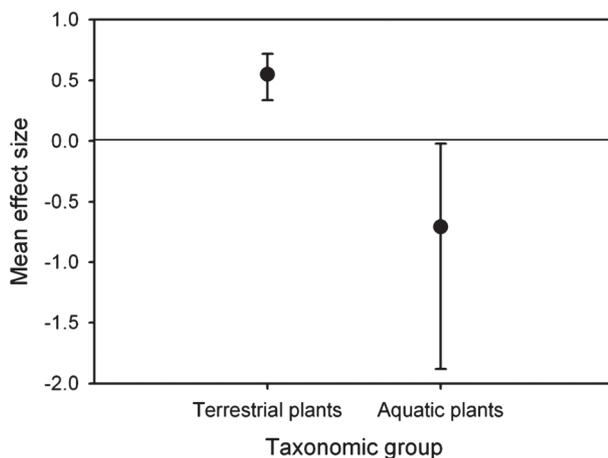


Figure 2. Results from the meta-analysis depicting production of invasive compared to native plants under low-nitrogen (N) conditions in aquatic and terrestrial ecosystems. Mean effect sizes (Hedges' d) \pm 95% of bootstrapped CIs are shown. Positive effect sizes indicate that the production of plants under low-N conditions is greater for invasive organisms as compared to natives. Confidence intervals that do not intercept zero indicate a significant difference between invasive and natives production based on $p < 0.05$. The difference between terrestrial and aquatic ecosystems was significant ($p < 0.05$).

than native plants under nutrient enrichment (Table 1B, Fig. 3). Although the responses of natives were mostly negative, they were not significantly different from zero, indicating that they did not respond to nutrient enrichment. Increased N:P ratios caused significant positive responses in production of both invasive and native plants, and the response was significantly greater for invasives (Table 1B). We did not have enough data to make comparisons between invasive and native responses to changes in N:P ratios among ecosystems.

Invertebrate invasions

Both invasive terrestrial and aquatic invertebrates showed significant positive performance responses (production, growth, and reproduction) to N- and P-enrichment of their food resource. In contrast, native invertebrates did not significantly respond to enrichment (Table 1B, Fig. 3). Under N-enrichment, the production of invasives was significantly different from that of native organisms (Table 1B, Fig. 3). Increased food N:P ratios caused significant, positive responses in the production of invasive invertebrates but not natives (Table 1B).

Due to the small sample size in the aquatic dataset, we could not compare the performance of invasive and native invertebrates in different aquatic ecosystems (i.e. freshwater vs marine). However, among terrestrial ecosystems, production response of invasive and native invertebrates to N availability in their food resources differed among temperate grasslands, tropical forests and agro-ecosystems (Fig. 4). In temperate grasslands, invasive invertebrates had a positive response to higher N availability, whereas the production of native invertebrates under increased N was negative. In contrast, invasive and native invertebrate production in tropical forests had negative responses under increased N supply, although these differences were not statistically significant from zero for both. In addition, production response of invasive invertebrates in agro-ecosystems was greater with increased N availability (no available data for native invertebrates). We did not have enough data to explore patterns under different P availabilities.

Discussion

The results of our meta-analyses support the hypothesis that invasive organisms are able to outperform natives in low-resource environments. Our data therefore challenge the idea that native organisms generally outperform invasives in low-resource environments (Daehler 2003). However, the higher response of invasive organisms compared to natives was restricted to terrestrial plants, whereas aquatic plants showed the opposite pattern. The results from terrestrial plants are in agreement with a recent empirical study by Funk and Vitousek (2007) that compared leaf-level physiological traits associated with RUE in 19 pairs of phylogenetically related invasive and native terrestrial plant species from three resource-limited habitats in Hawai'i. They found that invasive plants were generally more efficient than native plants at using limited resources.

According to our model, invasive plants are able to succeed under low-nutrient conditions because they display higher resource acquisition, lower nutrient requirements and also less resource-limited growth as compared

Table 1. Results of meta-analyses comparing invasive and native plant and invertebrate response variables (production, growth, reproduction) to (A) increased carbon:nitrogen (C:N) and carbon: phosphorus (C:P) ratios, (B) increased nitrogen (N), phosphorus (P) concentrations and nitrogen: phosphorus (N:P) ratios in terrestrial and aquatic ecosystems. Values are effects sizes ($\pm 95\%$ bootstrapped confidence intervals), Bold values have CIs that do not overlap zero, “-” indicates data missing from literature, ‡ indicates insufficient data for robust meta-analyses results

| | C:N | | C:P | |
|----------------------|-----------------------|-----------------------|-------------------------|----------------------|
| | Invasive | Native | Invasive | Native |
| <u>Plants</u> | | | | |
| Aquatic | - | - | - | - |
| production | - | - | - | - |
| growth | - | - | - | - |
| <u>Invertebrates</u> | | | | |
| Terrestrial | -0.51 (-0.83 to 0.14) | -0.17 (-0.43 to 0.10) | 1.58 (-1.79 to 2.25)* | 0.10(-0.64 to 0.84)* |
| production | - | - | - | - |
| growth | - | - | - | - |
| reproduction | - | - | -1.27 (-2.69 to -1.119) | - |
| Aquatic | - | - | - | - |

| | N | | P | | N:P | |
|----------------------|-------------------------------|-------------------------|------------------------------|-----------------------------|-----------------------------|-----------------------------|
| | Invasive | Native | Invasive | Native | Invasive | Native |
| <u>Plants</u> | | | | | | |
| Terrestrial | 0.40 (-0.13 to 0.82) | -0.13 (-0.38 to 0.19) | 0.26 (0.10 to 0.44)** | -0.17 (-0.33 to 0.10)** | - | - |
| production | 2.29 (0.83 to 5.57)** | 0.01 (-0.30 to 0.31)* | - | - | - | - |
| growth | 1.53 (0.981 to 2.57)** | -0.63 (-2.64 to 1.78)* | 1.25 (0.33 to 2.01) | 1.80 (1.09 to 3.28)* | 1.24 (0.22 to 3.26)* | 0.50 (-0.53 to 2.27) |
| Aquatic | 2.25 (1.15 to 7.18)** | 0.67 (-0.42 to 2.71)** | - | - | 0.27 (-0.18 to 0.56) | - |
| <u>Invertebrates</u> | | | | | | |
| Terrestrial | 0.92 (0.35 to 1.29)** | -0.11 (-0.29 to 0.83)** | 0.06 (-0.71 to 0.63)‡ | -0.25 (-0.65 to 0.14)‡ | 0.68 (0.64 to 0.71) | 0.15 (-0.19 to 0.44) |
| production | 1.94 (1.76 to 2.19) | - | 1.94 (0.35 to 2.09) | - | - | - |
| growth | 1.16 (0.35 to 2.88) | - | 1.16 (0.36 to 2.09) | - | - | - |
| reproduction | 1.10 (1.05 to 1.16) | - | 0.91 (0.4 to 1.42) | - | - | - |
| Aquatic | - | - | - | - | - | - |
| production | - | - | - | - | - | - |
| growth | - | - | - | - | - | - |
| reproduction | - | - | - | - | - | - |

Student t-tests comparing invasive and native effect sizes *p < 0.05, **p < 0.01, ***p < 0.001

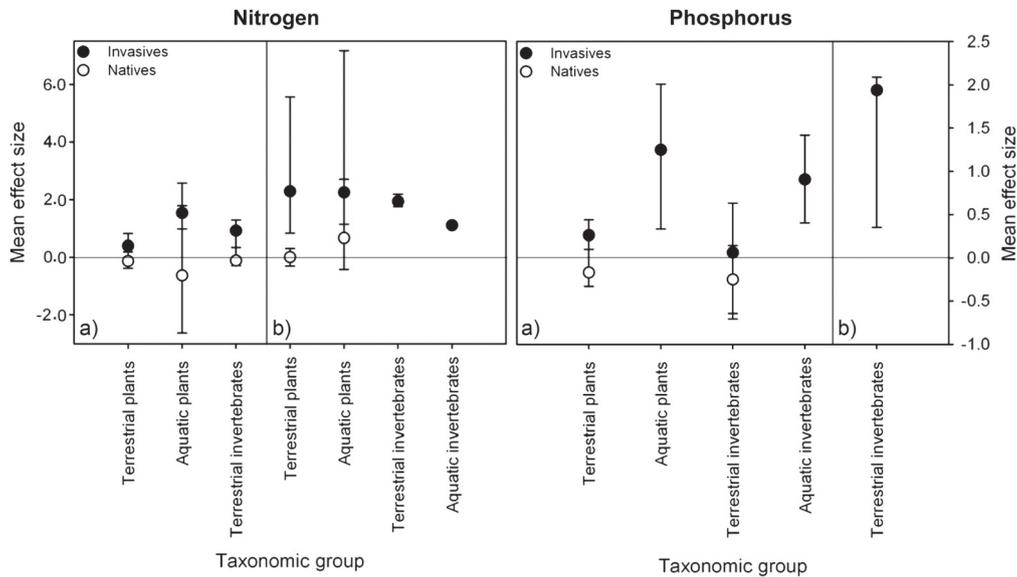


Figure 3. Results from the meta-analysis depicting performance of invasive and native organisms under nutrient enrichment. The manipulated nutrients were nitrogen (left panels) and phosphorus (right panels). The performance variables shown are a) production and b) growth rate for invasive (closed circle) and native (open circle) organisms. Mean effect sizes (Hedges' d) \pm 95% of bootstrapped CIs are shown. Confidence intervals that do not intercept zero indicate a significant effect of nutrient increase based on $p < 0.05$. See Table 1 for the estimated significance levels of Student's t -test for the difference between invasive and native organisms performance under nutrient enrichment.

to natives (lower R^* ; Tilman 1982, Shea and Cheeson 2002, Daehler 2003). Further, invader success under low-nutrient availability is enabled by lower allocation of nutrients to constitutive defenses and an increase in resource allocation to growth and reproduction (Blossey and Notzold 1995, Agrawal 2001, Blumenthal 2006). Enemy-release effects are also expected to increase with the degree of enemy specialization (Keane and Crawley 2002, Parker and Hay 2005, Vermeij et al. 2009). Herbivores in terrestrial systems are often highly specialized, whereas in aquatic systems many herbivores are trophic generalists with a low degree of diet specialization (Shurin et al. 2006). Thus, higher effects of release from specialized herbivores might therefore explain why invasive organisms outperform natives in terrestrial ecosystems but not in aquatic ecosystems.

At lower nutrient levels, invasive invertebrates responded more negatively to increased food C:N ratios (although not significantly) and more positively to increased food C:P ratios than natives. Our results suggest that on average invasive organisms could be more N- than P-limited (i.e. have lower C:N-TER and/or higher C:P-TERs relative to natives). Further, some invertebrates (e.g. zebra mussels) are able to change their tissue nutrient stoichiometry (nutrient requirements, R^* extended to invader animals), in response to the variation in elemental composition of their food (Naddafi et al. 2009). Invaders that are more able to modify their nutrient requirements and grow faster per unit nutrient used than natives will have a competitive advantage in these nutrient-poor environments. These findings suggest that invaders could overcome the stoichiometric constraints of their food resources through changes on their nutrient requirements and TERs, and then maintain themselves (growing and reproducing) on a low-nutrient level, thereby increasing their competitive ability compared to natives.

Invasive and native organisms under nutrient-enriched conditions

The results from our second meta-analysis support our model predictions that invasive organisms outperform natives under nutrient enrichment (N and P) (Fig. 1). Both N- and P-enrichment enhanced plant and invertebrate invasion success.

In general, our findings help to clarify previously conflicting research connecting biological invasion success to nutrient availability. Some studies have found that invasive organisms outperform natives under high-nutrient conditions (Chun et al. 2007, Hastwell et al. 2008), whereas others have found no effect of nutrient enrichment on invasion success (Hastwell and Panetta 2005). Some of our results were consistent with the hypothesis of increased resource availability promoting invasion (Davis et al. 2000). For example, we showed that there was variation among terrestrial ecosystem types (temperate grasslands, tropical forests, agricultural ecosystems) in response to nutrient availability for invertebrates. Temperate grassland and agricultural ecosystems showed positive invertebrate production responses to N enrichment, whereas in tropical forests both invasive and native invertebrates responded negatively to increased N. Tropical ecosystems are predominately limited by P (Rosemond et al. 2001, 2002, Reich and Oleksyn 2004, but see Elser et al. 2007), and increased P-limitation due to N enrichment may impose stronger constraints on the growth and reproduction of consumers (Rosemond et al. 2001, but see Elser et al. 2007). In temperate ecosystems, additional N deposition will likely stimulate performance of invasive organisms over natives (LeBauer and Treseder 2008). Previous studies indicate that N enrichment reduces competition and enhances ecosystem invasibility (Huenneke et al. 1990, Milchunas and Laurenroth 1995, Maron and Connors 1996, Davis and Pelsor 2001). However, as both

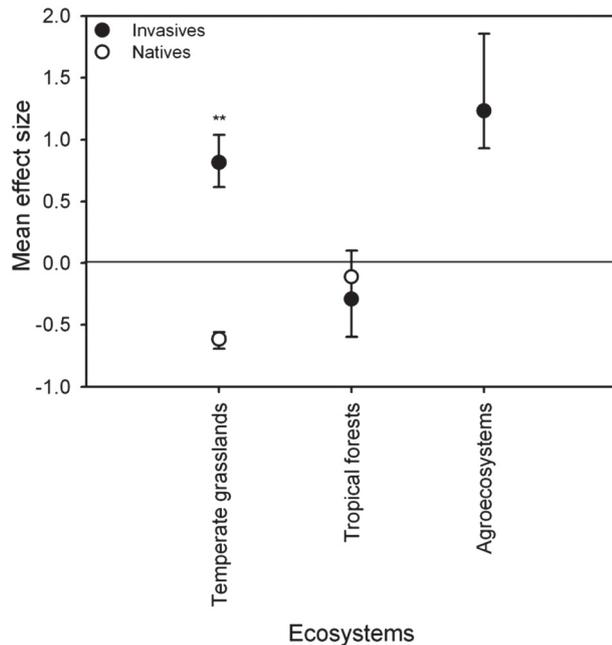


Figure 4. Results from the meta-analysis depicting production of invasive compared to native invertebrates under nitrogen (N) enrichment in terrestrial ecosystems. Mean effect sizes (Hedges' d) \pm 95% of bootstrapped CIs are shown. Confidence intervals that do not intercept zero indicate a significant effect of nutrient increase based on $p < 0.05$. The difference between invasive and native organism production was significant (** $p < 0.01$).

native and invasive organisms can profit from enrichment, increased resource availability alone may be insufficient to explain patterns of invasion success (Blumenthal 2006).

According to the GRH (Elser et al. 2003), fast-growing organisms tend to have low body C:P and N:P ratios due to higher P-rich ribosomal RNA production required to meet their elevated protein synthesis demands of rapid growth and development. Based on this hypothesis we propose that at higher nutrient availabilities, invasive organisms will have higher growth rates and/or reproductive output compared to natives. However, the large allocation of P required in fast-growing organisms (e.g. invasives) suggests that these organisms might also be more likely to be P-limited (Sternler and Elser 2002). Additional support of the main role of GRH explaining invasive success is given by Acharya et al. (2006) who found a higher tissue %RNA and %P linked to higher reproductive outputs of *Daphnia lumholtzi* in P-rich ecosystems compared to native zooplankton. Similarly, Smith et al. (2009) showed that *D. lumholtzi* growth rates and reproductive outputs declined significantly under low-P availability. Therefore, nutrient-rich ecosystems might facilitate *D. lumholtzi* invasions, whereby it takes advantage of available nutrients more efficiently than native organisms. Nonetheless, empirical evidence also shows that *D. lumholtzi* out-competed native taxa under low-P availability (Dzialowski et al. 2000, Wang et al. 2009) because of their lower nutrient requirements for growth and higher C:P-TERs than natives (Wang et al. 2009). Correspondingly, Lennon et al. (2003) reported that *D. lumholtzi* density decreased under higher-P availability but was greater at low-P supply. These findings indicate that invasive *D. lumholtzi* might not be constrained by a low availability of nutrients but may outperform natives

depending on community structure, temperature or inducible defenses against predators (Dzialowski et al. 2003, Lennon et al. 2003, Engel and Tollrian 2009, Wang et al. 2009). The current lack of abundant empirical evidence precludes any theoretical generalizations. We highlight the case of *D. lumholtzi* as it appears to be an interesting and rare example of invasion across a range of nutrient availabilities by displaying different stoichiometric-based traits, such as higher growth rate under high P-availability (GRH), and higher C:nutrient-TERs and adaptive trait plasticity in its nutrient requirements in response to increased food C:P ratios.

In our conceptual model, we suggest that invasion success is enhanced by a synergistic interaction between resource-enemy release (Blumenthal 2006) and stoichiometric-based mechanisms. For example, the effect of a natural enemy on plants can be stronger in high- than in low-resource environments because high-nutrient organisms tend to have higher tissue nutrient content (lower tissue C:nutrient ratios) and lower structural and chemical defenses, which increases herbivory pressure (Coley et al. 1985, Blumenthal 2006). In addition, high-nutrient resources (low food C:nutrient ratios) can promote pathogen infection of hosts (Frost et al. 2008). Invasive organisms may therefore benefit from both pathogen release as well as high-resource availability (Blumenthal et al. 2009).

Biological invasions under low- and high-resource levels

Our proposed framework integrates different mechanistic explanations of invasion success using principles of ES to explain the relative performances of invasive compared to native organisms at contrasting resource availabilities; low- and high-resource environments. In low-resource environments, a predominant trait of successful invaders is higher C:nutrient content and thus lower nutrient requirements for growth and reproduction (lower R^*). For organisms with lower nutrient requirements (e.g. high TER), invasion success will only occur in environments that support the resource requirements of those traits. However, for organisms with plastic traits, we could expect changes in its nutrient requirements to maintain higher growth rates and subsequent invasion success across ecosystems. In high-nutrient environments, invaders should have lower tissue C:nutrient ratios than natives, which is linked to higher growth rates (Elser et al. 2003). Thus, in nutrient-rich environments we suggest that organisms with higher growth rates and reproductive outputs have an increased probability of being superior competitors (e.g. invasive organisms; Stachowicz and Tilman 2005, Schumacher et al. 2009). According to the GRH, these organisms are expected to have low C:nutrient ratios, mainly driven by high nutrient requirements for growth. Results from our meta-analyses provide evidence that invasive organisms are successful in both low- and high-nutrient conditions, which must be explained by different mechanisms.

The principles of ES might also explain why most introduced organisms fail to become invasive in ecosystems. Invasion success requires that: 1) non-native organisms meet their demands for N and P either through a higher C:nutrient-TER (under low- nutrient levels) or higher nutrient sequestration

compared to natives, 2) introduced organisms are able to out-compete natives through higher growth rates (GRH; Elser et al. 2003), and 3) non-native organisms have either low tissue C:nutrient ratios and/or fewer natural enemies present in the invaded environment (Frost et al. 2008, Blumenthal et al. 2009). We therefore suggest that unsuccessful invaders lack one or more of these stoichiometric-based mechanisms or do not display adaptive changes in stoichiometric traits (Naddafi et al. 2009). Thus, characterizing successful and unsuccessful invasions under ES principles could provide deeper understanding of underlying mechanisms driving invasion success.

Overall, our meta-analyses indicate that biological invasions can occur in both nutrient-poor and nutrient-rich ecosystems, but imply that the traits of invasive organisms that succeed in low- versus high-nutrient environments should differ in predictable ways. For example, the invasive nitrogen-fixing tree *Myrica faya*, invades N-limited, P-rich ecosystems (Vitousek 2004). Nitrogen-fixing organisms do not succeed under P- limitation because nitrogen fixation requires high availability of P, constraining the success of these organisms in low-nutrient ecosystems (Smith 1992, Vitousek 1999, Finzi and Rodgers 2009). Based on this rationale, 'resource competition theory' has been directly applied to control invasive organisms (Newingham and Belnap 2006). The question that arises is: could an invasive organism that is adapted to high-N conditions in its native range succeed under low-N supply in the invaded ecosystem or vice versa? Based on previous research, it appears that invaders with consistently higher performance than natives across broad environmental conditions are uncommon (Daehler 2003).

Although we did not discuss rapid evolutionary change of traits related to invasiveness in invaded ecosystems (e.g. growth rates, generation time, reproductive output and competitive ability), increasing evidence indicates that such changes have mainly a synergistic effect by increasing invasion potential (Blair and Wolfe 2004, Whitney and Gabler 2008). Hence, the multiple successive introductions and high population growth rates of many invaders are expected to promote adaptive evolution (Reznick and Ghalambor 2001, Suárez and Tsutsui 2008).

Further, theoretical and empirical evidence suggest that invading populations are excellent examples of adaptive evolutionary change (Richards et al. 2006, Whitney and Gabler 2008). Actually, recent progress in understanding evolutionary implications of ES has pointed out that traits related to stoichiometry such as body nutrient content and growth rate show high plasticity and also would undergo evolutionary change (Gorokhova et al. 2002, Jeyasingh and Weider 2005, 2007, Kay et al. 2005, Elser 2006). Therefore, it is fundamental to examine how stoichiometric-based traits in invasive organisms could evolve to potentially increase their success.

Concluding remarks

Our study proposes the novel integration of previous hypotheses of biological invasions within a structured and formal framework based on the principles of Ecological Stoichiometry. In addition, we have elucidated that differences in patterns of biological invasions exist between terrestrial and aquatic ecosystems and that invasive organisms are successful at both low- and high-resource levels. These results, in

conjunction with our conceptual model predictions, suggest that nutrient availability, organism nutrient requirements (i.e. tissue C:N ratios, R^* , C:nutrient-TERs), growth rates (GRH), adaptive plasticity and enemy release may interactively increase invasion potential across taxa (producers and consumers) and across ecosystems.

Insufficient data for all possible combinations of nutrients and ecosystems often prevented us from comparing performance responses of invasive and native organisms from a larger suite of ecosystem types. Therefore, additional empirical studies, especially factorial experimental manipulations of nutrient availability and enemies would improve our ability to test the proposed stoichiometric-based mechanisms. Further, estimates of C:N:P stoichiometry of invasive and native organisms across natural and controlled gradients of nutrient availability remain fairly unknown and raise questions about patterns and mechanisms underlying invasive organism stoichiometry. One of the challenges for future research is to understand whether or not stoichiometric constraints differ between invasive and native organisms and to evaluate empirically the role of stoichiometric-based mechanisms proposed here in determining invasion success. Another challenge entails addressing the role of other elements such as Fe, Mo, Ca and Mg, in limiting growth and reproduction of invasive taxa across ecosystems. Finally, the ES framework could also be applied to understand the consequences of biological invasions for ecosystem structure and functioning, and how global change drivers such as nutrient deposition and elevated CO₂ might affect the invasiveness of organisms and the invasibility of ecosystems. Ecological stoichiometry provides a unifying conceptual framework that can improve our general understanding of the phenomenon of biological invasions across nutrient availabilities and ecosystem types.

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Supplementary material (available online as Appendix O18549 at <www.oikos.ekol.lu.se/appendix>). Appendix 1