

Redundancy and niche differentiation among the European invasive *Elodea* species

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Abstract Community ecologists implicitly assume redundancy when they aggregate species into functional groups. But there have been remarkably few empirical efforts to investigate the accuracy of this concept in situ. The concept of redundancy could be roughly split into two components: the ecological redundancy (similar response to environmental variations involving similar ecological processes) and the functional redundancy (similar biological trait combinations shaping similar functional processes). Both types of redundancy are tested among the 3 invasive European *Elodeas*. In 11 sites and during two successive years 2004–2005, the cover growth rate of each *Elodea* species was monthly recorded. To test ecological redundancy, cover growth rates were related to a large suite of environmental variables. To test functional redundancy, 13 biological traits involved in competitive relationships were measured each month. Firstly, the redundancy hypothesis looks problematic for *Elodea ernstiae*. Indeed, the later possess numerous biological traits involved in light competition and niche overlap with the other *Elodeas* is very low. Secondly, ecological and functional

redundancy can be successfully applied to *Elodea canadensis* and *Elodea nuttallii*. They share a large suite of biological traits leading to wide niche overlaps through the growing season. And the measured environmental variables do not differentially influence their growth rates, which are, in turn, controlled by a similar group of biological traits. In this way, the different invasiveness patterns of *E. canadensis* and *E. nuttallii* could be solely due to the ecological drift and their ecological dynamic could follow neutral rules.

Keywords Biological traits · Functional equivalence · Invasiveness · Niche overlapping · Waterweeds

Introduction

The concept of species redundancy was introduced in detail by Walker (1992) with biodiversity conservation goals but has roots extending back to the idea of ecological guilds (Root 1967), i.e. grouping together organisms based on convergence in what they do in ecological systems. Where there is more than one species in a guild, these species would be redundant (Gitay et al. 1996). This means that different species have the same role in the system (Naeem 1998) so that changes in species diversity, i.e. loss or gain of redundant species, should not affect ecosystem functioning (Loreau 2004). Despite this simple definition,

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redundancy is difficult to assess unambiguously as it involves several dimensions of the species niche (Rosenfeld 2002). The latter can be defined in terms of functional (physiological, morphological, phenological...) processes related to specific biological traits (the functional niche) and in terms of environmental factors that will mediate how an organism can perform its functional processes (the ecological niche). Theoretically, redundant species should overlap in both dimensions, which can thus be used as criteria for assessing redundancy. Community ecologists commonly assume redundancy when they aggregate species from similar trophic levels into functional groups (Hubbell 2005). However, there have been remarkably few theoretical (Loreau 2004) and empirical (Hubbell 2005) efforts to investigate the accuracy and applicability of this concept in natural ecological systems (Hérault in press). Moreover, the growing literature on functional groups is curiously silent about the assumption of species redundancy within functional groups while being remarkably prolix about the ideas of niche differentiation between functional groups (Hubbell 2005).

The aim of this study is to investigate redundancy among the invasive European *Elodeas*. In Europe, the genus *Elodea* consists of 3 distinct species: *Elodea canadensis* Michx., *Elodea ernstiae* H. St. John and *Elodea nuttallii* (Planch.) H. St. John. The three species are morphologically similar, all having long, flexuous leafy stems rooted in the substratum in spring, but often becoming detached later in life (James et al. 1999). Reproduction is vegetative as most European populations are female. They share a large suite of biological traits (anchored, submerged leaves, multiple apical growth points, leaf area lower than 1 cm², propagation using fragmentation, rigid and non-waxy leaf texture and water-pollination in its original area) owing to their close phylogenetic history (Willby et al. 2000). *Elodea canadensis* was first introduced into the British Isles in the nineteenth century and became a widely distributed species throughout Europe during the twentieth century (Simpson 1984). *Elodea canadensis* has a wide latitudinal range and extends from peaty to calcareous sites and from mesotrophic to eutrophic waters. The introduction of *E. nuttallii* into the British Isles and next into continental Europe has resulted in the displacement of *E. canadensis* from several waters where the former had become common (Greulich and

Trémolières 2006; Simpson 1990). Finally, *E. ernstiae* is locally recorded at lower abundance and generally remains discreet enough in aquatic communities.

Why these species with a priori similar niches, similar morphological forms and similar reproductive strategies display different invasiveness patterns? Many hypotheses have been proposed to explain why some organisms are more invasive than others (Callaway and Aschehoug 2000; Kolar and Lodge 2001; Shea and Chesson 2002). Among others, the enemy release hypothesis attributes the success of exotic species to their escape from diseases and herbivores (Keane and Crawley 2002; Klironomos 2002; Van der Putten 2002). On the other hand, many hypotheses have been proposed to explain why some communities are more invaded than others: the fluctuating resource hypothesis (Davis et al. 2000), the invasibility hypothesis (Kennedy et al. 2002; Lonsdale 1999) or the global change hypothesis (Didham et al. 2005). But no general theory has emerged up to now and it looks very unlikely that any single theory will be able to account for all cases of invasiveness (Blumenthal 2005). Regarding the European *Elodeas*, number of laboratory studies have attempted to explain the apparent competitive success of *E. nuttallii* in displacing *E. canadensis* (e.g. Barrat-Segretain 2005; Barrat-Segretain et al. 2002; James et al. 2006). Up to now, these laboratory studies have largely demonstrated that some features do not appear to be important. First, the environmental conditions tolerated by these two species widely overlap (James et al. 1999; Jones et al. 2000). Both species show similar resistance to water current (Barrat-Segretain et al. 2002). No clear differences in photosynthetic behaviour (James et al. 1999) and in species responses to nutrient enrichment (James et al. 2006) were observed. Their abilities to regenerate and colonize using vegetative fragments are quite similar and the palatability of *E. nuttallii* is slightly higher than that of *E. canadensis* but does not likely explain the observed field-displacements (Barrat-Segretain et al. 2002). On the whole, the above laboratory studies have led to the conclusion that the *Elodeas* share a common ecological niche. They may therefore be substitutable and considered as true redundant species, in the laboratory at least. However, the applicability of the concept of ecological redundancy should also be tested in field conditions as it could be a wide gap between the fundamental and the realized

Table 1 Overview of the monthly-recorded environmental variables selected to test the ecological redundancy among European *Elodeas*

Variable name	Analytic methods and variable range
<i>Abiotic variables</i>	
[Cl ⁻]	Ionic chromatography Dionex DX 120; from 16.4 to 51.1 mg l ⁻¹
Conductivity	Field-measured with a specific electrode; from 250 to 587 µS cm ⁻¹
[N-NH ₄ ⁺]	Spectrophotometric autoanalyser; from 2 to 208 µg l ⁻¹
[N-NO ₃ ⁻]	Ionic chromatography Dionex DX 120; from 0.11 to 3.26 mg l ⁻¹
[O ₂]	Field-measured with the Oxymeter WTW; from 4.6 to 22.9 mg. l ⁻¹
pH	Field-measured with the pH meter WTW; from 7.20 to 9.27
[P-PO ₄ ³⁻]	Spectrophotometric autoanalyser; from 1 to 49 µg l ⁻¹
[S-SO ₄ ²⁻]	Ionic chromatography Dionex DX 120; from 19.2 to 33.6 mg l ⁻¹
Temperature	From 6.1 to 25.1°C
<i>Biotic variables</i>	
<i>Elodea canadensis</i>	Change in plant cover; from -0.39 to 0.34% cover day ⁻¹
<i>Elodea ernstiae</i>	Change in plant cover; from -0.540 to 1.162% cover day ⁻¹
<i>Elodea nuttallii</i>	Change in plant cover; from -0.495 to 2.000% cover day ⁻¹
Vascular plant cover	Sum of the percentage cover of all vascular plants; from 0 to 152%
Non-vascular plant cover	Sum of the percentage cover of all non-vascular plants; from 0 to 398%

niche (McGill et al. 2006). To test whether or not the European *Elodeas* can be considered as true ecological and functional redundant species, we made a suite of predictions, which were tested in situ. First, the *Elodeas'* cover growth rates should be predicted by the same suite of environmental variables (H1), including the cover growth rate of the other *Elodea* species (competitive interactions typical of true redundant species). Next, the values of their biological traits should widely overlap if they performed a similar role in the river system and this functional overlapping should not vary with the increased competition due to vegetation development during the growing season (H2). Finally, variations in cover growth rates should involve similar biological traits if the 3 *Elodeas* respond to environmental fluctuations using similar functional processes (H3).

Materials and methods

Data collection

The study sites were located in the Rhine former floodplain (Eastern France) where the 3 *Elodeas* co-occured. Data were collected in 11 sites (selected to obtain a broad range of physico-chemical

variables) for two successive years 2004–2005. In each site, three randomly chosen transects (2 m wide each) crossing the river were established. During the year 2004, all transects were precisely surveyed once a month from March to November. Each *Elodea* species as well as the other vascular and non-vascular plants received a cover percentage. To avoid pseudo-replication problems (Hurlbert 1984), data were averaged by sites in the following analyses. Simultaneously, a large suite of water variables were monthly recorded (Table 1).

During the year 2005, cover percentages were again measured in situ. In each site, 20 rooted ramets from each *Elodea* species were sampled once a month. A large suite of biological traits was then measured on each ramet (Table 2). The selected traits are commonly used to investigate competitive relationships and reflect key-features in plant development (Weiher et al. 1999; Willby et al. 2000). Leaf areas were measured (using the image analysing software ImageJ, <http://www.rsb.info.nih.gov/ij/>) on a leaf picked just below the apex where leaves are fully expanded and internodes regularly spaced. Biological traits such as internode's length (Stem length/Node number), dry density (Dry mass/Total length), branching degree (Branch number/Stem length) and lateral spread (Total length/

Table 2 Overview of measured and derived^a biological traits measured to test the functional redundancy among European *Elodea*

Traits	Description
Branch number	Lateral shoots were counted when they were at least 5 mm long
Dry mass	Including all shoots and leaves
Leaf areas	Measured using the software ImageJ
Stem length	Length from the base of the ramet to the apex
Node number	Number of nodes of the stem
Root number	Roots were counted when they were at least 1 mm long
Total length	Including all shoots

^a Other secondary traits derived from measured traits:

Internode's length = Stem length/Node number

Dry density = Dry mass/Total length

Branching degree = Branch number/Stem length

Lateral spread = Total length/Stem length

Foliar investment = 3 Leaf areas/Internode's length

Stem length) were derived from measured traits. As *Elodea* shoots are composed of a suite of regularly spaced nodes with three similar-sized leaves each, foliar investment was estimated by dividing three leaf areas by one internode's length.

Statistical analyses

Given that the cover percentage of each *Elodea* was recorded once a month in each site, a daily-change in cover percentage was easily calculated. This index was named Cover Growth Rate (CGR in the following). CGRs, environmental factors and biological traits had predictable yearly fluctuations. For example, $[\text{N-NH}_4^+]$ was high in March, decreased from April to July and then increased again. To extract these trends for data analysis, monthly medians were always taken away from original values. Next, residuals were checked for normality and Dry masses, Branch numbers and Number of nodes were log-transformed while Stem lengths and Total lengths were squared-root.

H1: Three General Linear Models were used to relate environmental factors to variation in CGR for the *Elodea* *i*:

$$\text{CGR}_{(i,j)} = \sum_{j=1}^e E_{ij} + \varepsilon \quad (1)$$

where e is the number of environmental factors, E the numerical values for the factor j and ε the model residuals. The stepwise procedure (Legendre and Legendre 1998) was applied to choose the best model including the significant factors j only.

H2: One-way analyses of variance were first done to test the influence of the species identity on trait values. Next, we estimated the overlap of trait T between *Elodea* i and *Elodea* j by the usual formula for the overlap of two normal distribution (Mouillot et al. 2005):

$$\text{NO}_{T(i,j)} = e^{\frac{-(\mu_i - \mu_j)^2}{2(\sigma_i^2 + \sigma_j^2)}} \quad (2)$$

where μ_i mean (= mode = median) of the distribution of species i , μ_j mean of the distribution of species j , σ_i^2 variance of the distribution of species i , σ_j^2 variance of the distribution of species j . Finally, trait overlaps NO_T were averaged by month and species couple (i,j) to obtain functional niche overlap values. To obtain confidence interval through the sampling distribution of the mean, we used bootstrapping techniques by resampling (1,000 re-samples) the individuals without replacement (Manly 1998).

H3: Three Generalized Linear Models were used to relate biological traits to variation in CGR for the *Elodea* i :

Table 3 Ecological redundancy^a among the European *Elodeas*

Response variable	Predictors	Wald statistic	P	Coefficient
<i>Elodea canadensis</i>	<i>Elodea nuttallii</i>	16.18	***	-1.71
	Non-vascular plant cover	7.20	**	-1.01
	[S-SO ₄ ²⁻]	6.11	*	1.95
<i>Elodea ernstiae</i>	None			
<i>Elodea nuttallii</i>	<i>Elodea canadensis</i>	18.59	***	-1.98
	Non-vascular plant cover	7.52	**	-1.54
	[S-SO ₄ ²⁻]	6.62	*	3.88

^a Cover Growth Rates were related to environmental variables using Generalized Linear Models with step-wise selection procedures
 * $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$; ns—not significant

$$CGR_{(i,j)} = \sum_{j=1}^t T_{ij} + \varepsilon \tag{3}$$

where t is the number of environmental factors, T the numerical values for the trait j and ε the model residuals. To choose the best parsimonious model including the significant trait j only, the Akaike Information Criterion was used in a stepwise algorithm.

Statistical analyses were done using R (<http://www.r-project.org/>).

Results

The stepwise procedure (H1) did not select a significant model to predict the cover growth rates of *E. ernstiae*. Models for *E. canadensis* and *E. nuttallii* were highly significant. Above all, the best predictor of the CGR of a given *Elodea* was the CGR of the other one (Table 3). Either both *Elodeas* had strong competitive interactions or a particular environmental predictor had a differential effect, i.e. favouring an *Elodea* while impeding the other one and *vice versa*. Among the environmental predictors shared by both models (Table 3), such a behaviour was not detectable. Indeed, while non-vascular plant cover impeded the CGR of both species, [S-SO₄²⁻] favoured the CGR of, again, both species.

Variations in biological trait values among the 3 *Elodeas* were assessed using Analyses of Variance

(H2). Several traits did not differ between the three species (Table 4). The other traits clearly separated *E. ernstiae* from the other 2 *Elodeas*. *Elodea canadensis* and *E. nuttallii* possessed low leaf areas, short internodes, numerous branches per unit of length and high dry densities. On the contrary, *E. ernstiae* showed few branches, low dry densities,

Table 4 Functional redundancy^a among the European *Elodeas*

	F	P
<i>Traits not significantly different between the 3 Elodeas</i>		
Stem length	3.16	ns
Root number	0.53	ns
Total length	0.38	ns
Foliar investment	1.24	ns
<i>Traits significantly different for Elodea ernstiae only</i>		
Internode's length	11.4	***
Branch number	9.56	***
Dry density	7.11	**
Dry mass	6.01	**
Leaf area	5.44	**
Node number	4.75	*
Branching degree	4.31	*
Lateral spread	6.23	**

^a Trait values were compared among *Elodeas* using one-way analysis of variance followed by Tukey post-hoc comparison tests

* $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$; ns—not significant

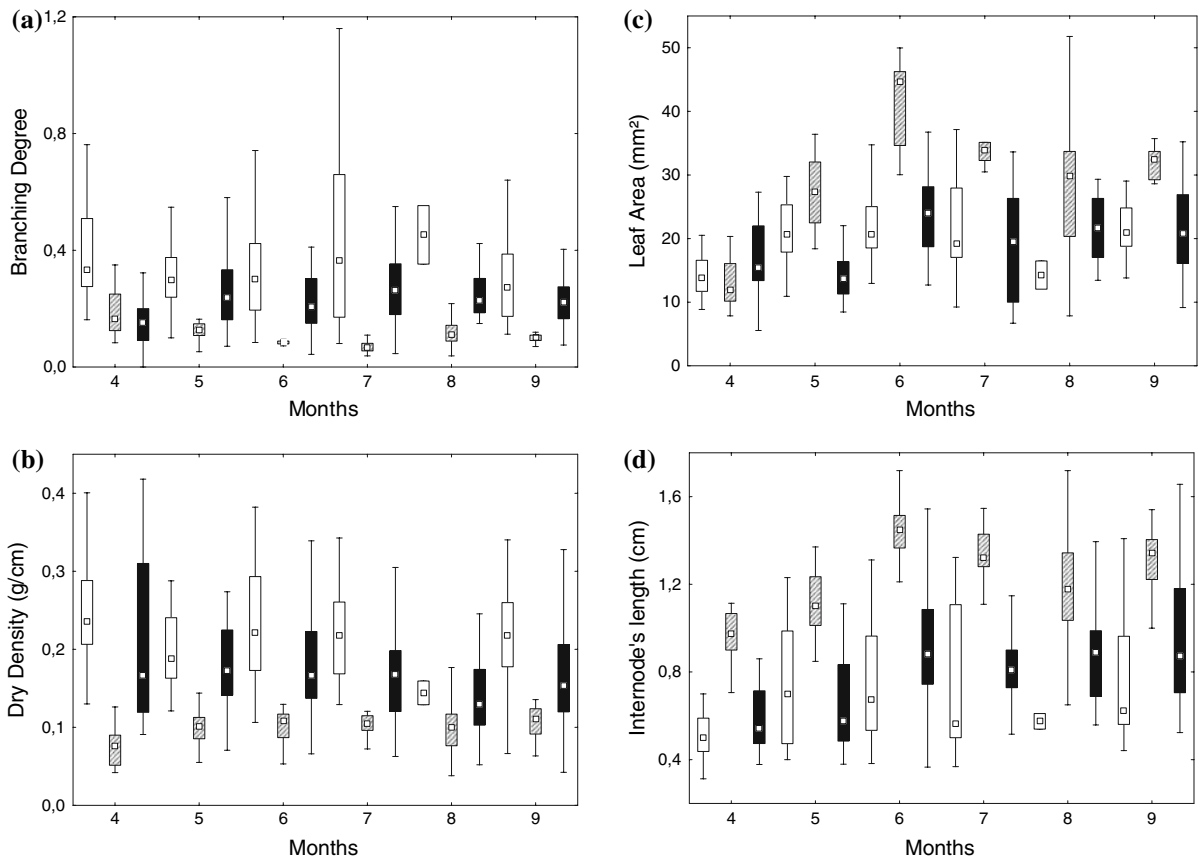


Fig. 1 Boxplots of biological trait values (**a**) branching degree, (**b**) dry density, (**c**) leaf area, (**d**) internode's length) versus months showing the original functional niche of *E. ernstiae*. White boxes: *E. canadensis*, Grey boxes: *E. ernstiae*, Black boxes: *E. nuttallii*

large leaves and very long internodes (Fig. 1). These differences were clearly put in light in the niche overlap analysis (Fig. 2). Niche overlap between *E. canadensis* and *E. nuttallii* was always close to 100%. On the other hand, niche overlaps between these two species and *E. ernstiae* were lower. Drops were very important when rates of vegetation development were high, i.e. between May and July.

Finally, the aim was to study how CGR variations were related to variations in biological traits (H3). On the whole, *E. canadensis* and *E. nuttallii* showed a very similar behaviour (Table 5). They increased leaf areas and internode's lengths but decreased foliar investment and stem length to boost their CGR. *Elodea ernstiae* had a completely different behaviour. Indeed, high CGRs were associated with high total lengths and high lateral spreads.

Discussion

Abiotic variables are far less important than biotic variables in predicting the growth rate of *E. canadensis* and *E. nuttallii* (Table 3). Ex situ, these *Elodeas* are well-known to respond in a similar way to a large suite of environmental fluctuations such as pH, Oxygen and dissolved inorganic carbon (Jones et al. 2000) as well as to different water current velocities (Barrat-Segretain et al. 2002). They have equivalent regeneration and colonisation abilities (Barrat-Segretain et al. 2002) and nutrient (P and N) enrichment does not have a central role in mediating their competition (James et al. 2006). In the same way, numbers of studies have also suggested that physiological responses to environmental fluctuations do not differ between *E. canadensis* and *E. nuttallii*. For instance, rates of photosynthesis and respiration

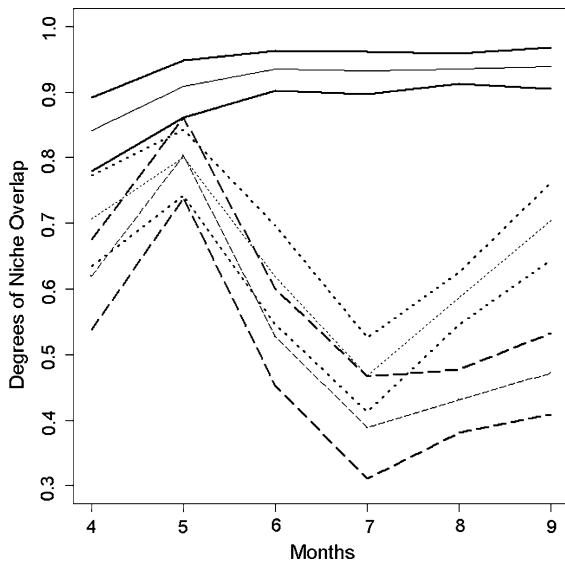


Fig. 2 Evolution of the degree of niche overlap between the 3 *Elodeas* during the period of vegetation development. Confidence intervals (in bold) were estimated using bootstrapping techniques. Plain lines: Niche overlap between *E. canadensis* and *E. nuttallii*; Dotted lines: Niche overlap between *E. ernstiae* and *E. nuttallii*; Dashed lines: Niche overlap between *Elodea ernstiae* and *E. canadensis*

under various conditions of pH, O₂ and dissolved organic carbon appear quite similar (Jones et al. 2000; Olesen and Madsen 2000). Our findings based on an intensive monitoring in the field confirm that environmental variables do not mediate this *intra-genus* competition (Table 3). However, no clear predictor of *E. ernstiae*'s CGR emerges and it may be possible that a wider range of factors than those studied here are involved in its growth. Nevertheless, the pivotal role of inter-specific competitive interactions is clearly highlighted for the two other *Elodeas*, validating H1 for these species.

It was already shown that *E. canadensis* and *E. nuttallii* have similar trait values regarding regeneration, resistance to water current velocity and palatability (Barrat-Segretain et al. 2002). The larger suite of biological traits investigated in this field-study completes the former results and clearly leads to the functional delineation of *E. ernstiae* (Table 4 and Fig. 1). The later is tall, weakly ramified, with leaves having high leaf areas and being widely spaced. On the other hand, *E. canadensis* and *E. nuttallii* are on average twice denser than *E. ernstiae*, have higher branching degrees, have smaller leaf areas and internode's length. As a result, the foliar

investment of *E. canadensis* and *E. nuttallii* is great. This supports the idea that *E. ernstiae* has a distinct functional niche (invalidating H2 for this species) regarding competition for light and this explain why niche overlap with the 2 other *Elodeas* is low (Fig. 2). Moreover, we demonstrate that niche differentiation occurs quickly during the period May–July when vegetation growth rates are the highest. This suggests that the degree of niche differentiation is closely linked to the degree of competition for light resources but this hypothesis needs further consideration. However, our results do not help to assign a functional niche to *E. canadensis* and *E. nuttallii*. The architecture of both species was roughly similar, and both species had the same light-competition biological traits. H2 is only validated for the couple *E. canadensis*/*E. nuttallii*.

Surprisingly enough, CGR variations in *E. ernstiae* are difficult to link with variations in biological trait values. This implies a very low morphological plasticity that can explain its very discreet behaviour in most aquatic communities. On the other hand, CGR variations in *E. canadensis* and in *E. nuttallii* are successfully related to several biological traits: internode's length, stem length, leaf area and foliar investment (Table 5, H3 validated for this couple). Such a pattern reflect the *Elodeas*' morphological plasticity, a feature already noted by Simpson (1988). A recent study (Di Nino 2002) has shown that this high morphological plasticity is firstly related to a high phenotypic plasticity, i.e. the ability of a single clone to produce highly differentiated phenotypes depending on environmental conditions (Miner et al. 2005; Sultan 2000). Phenotypic plasticity permits to produce a better phenotype–environment match to maximize fitness in variable conditions (Agrawal 2001). At this step, it should be remembered that the first predictor of *E. nuttallii*'s CGR is *E. canadensis*'s CGR, and vice-versa. In response to shading, *Elodeas* therefore decrease their foliar investment (Table 5 and Schlichting 1986) and elongate their internode's length to overtop direct competitors, a developmental response that brings their larger leaves (Table 5) into a more favourable light environment (Miner et al. 2005). However, phenotypic plasticity has an evolutionary cost with regard to maintenance, production, information acquisition and developmental instability (details in DeWitt et al. 1998) that may, in the long term, limit the success of these two invading *Elodeas*

Table 5 How variations in cover growth rates were linked to variation in trait values^a

	<i>Elodea canadensis</i>		<i>Elodea ernstiae</i>		<i>Elodea nuttallii</i>	
	<i>t</i>	<i>P</i>	<i>t</i>	<i>P</i>	<i>t</i>	<i>P</i>
Total length			3.45	***		
Lateral spread	-3.37	**	2.87	**		
Foliar investment	-3.45	***			-3.71	***
Leaf area	4.43	***			2.62	**
Stem length	-2.72	**			-5.54	***
Internode's length	2.96	**			5.97	***
Number of nodes					3.98	***

^a Trait values were related to Cover Growth rates using Generalized Linear Models with selection procedures based on the Akaike Information Criterion

* $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$; ns—not significant

and, ultimately, promote their coexistence with *E. ernstiae* (Gurevitch and Padilla 2004; Wilson and Yoshimura 1994).

Conclusion

This study aimed at questioning redundancy among European *Elodeas*. The concept of redundancy could be roughly split into two components: the ecological redundancy (i.e. whether the studied species respond similarly to environmental fluctuations) and the functional redundancy (i.e. whether the species share similar biological traits). We have shown that, among the three European *Elodeas*, two may successfully be considered as redundants: *E. canadensis* and *E. nuttallii*. On the other hand, strong competitive interactions have favoured the evolutionary divergence (Lee 2002) of *E. ernstiae*. Therefore, if a hard version of redundancy may be applied to *E. canadensis* and *E. nuttallii*, the emerging question is: How these species can coexist in the long term? Indeed, ecological theories based on the Lotka–Volterra competition model traditionally conclude that redundancy is incompatible with stable coexistence in the long term (Loreau 2004). However, Scheffer and van Nes (2006) have recently proposed an elegant theoretical solution to this problem: i.e. being sufficiently different or being sufficiently similar. Indeed, using a classical model of competition, they demonstrated a tendency for evolutionary emergence of regularly spaced lumps of similar species. In the long term, *E. canadensis* and *E. nuttallii* therefore appears

redundant enough to coexist within the lumps (Hérault in press). In this way, their different invasiveness patterns could be solely due to the ecological drift and their ecological dynamic could follow neutral rules (Hubbell 2001).

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