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ORIGINAL PAPER

Biodiversity influences invasion success of a facultative epiphytic seaweed in a marine forest

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Abstract The biotic resistance hypothesis predicts that more diverse communities should have greater resistance to invasions than species-poor communities. However for facultative and obligate epiphytic invaders a high native species richness, abundance and community complexity might provide more resources for the invader to thrive to. We conducted surveys across space and time to test for the influence of native algal species abundance and richness on the abundance of the invasive facultative epiphytic filamentous alga *Lophocladia lallemandii* in a Mediterranean *Cystoseira balearica* seaweed forest. By removing different functional groups of algae, we also tested whether these relationships were dependent on the complexity and abundance of the native algal community. When invasion was first detected, *Lophocladia* abundance was positively related to species richness, but the correlation became negative after two years of invasion. Similarly, a negative relationship was also observed across sites. The removal experiment revealed that more complex native communities were more heavily invaded, where also a positive relationship was found between native algal richness and *Lophocladia,* independently of the native algal abundance. Our observational and experimental data show that, at early stages of invasion, species-rich seaweed forests are not more resistant to invasion than species-poor communities. Higher richness of native algal species may increase resource availability (i.e.

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substrate) for invader establishment, thus facilitating invasion. After the initial invasion stage, native species richness decreases with time since invasion, suggesting negative impacts of invasive species on native biodiversity.

Keywords Benthic community · Invasibility · *Cystoseira* · Epiphytic · Functional groups · *Lophocladia* · Mediterranean marine community · Removal experiment · Seaweed

Introduction

Invasion success depends on biotic and abiotic factors that interact across temporal and spatial scales (Lonsdale 1999) and their effects vary throughout the different invasion phases (i.e., introduction, establishment and spread) (Theoharides and Dukes 2007). For example, during the introduction phase, successful colonization strongly depends on propagule pressure: the higher the number of introduction episodes and the greater the number of propagules per introduction, the greater the chance of a successful colonization (Simberloff 2009). Once the exotic has been established, invasion success varies widely among recipient communities (Levine and D'Antonio 1999; Lonsdale 1999; Kennedy et al. 2002).

Community traits that may influence habitat invasibility have been deeply explored. By one side, the biotic resistance hypothesis predicts that more diverse communities should be less susceptible to invasion because of an initial strong, competition-driven biotic resistance at small scales (i.e., Elton 1958; Kennedy et al. 2002; Van Ruijven et al. 2003), although studies at large scales have found that species-rich communities can be as prone to invasion as species-poor communities (Robinson et al. 1995; Capers et al. 2007). A meta-analysis across many terrestrial habitats (from grasslands to forests) shows that the relationship between invasion success and diversity is habitat dependent (Vilà et al. 2007), with hot spots of native diversity in undisturbed habitats, such are mature forests, being invaded by many exotic plant species (Rejmánek 1996; Fine 2002; Howard et al. 2005; Brooks and Jordan 2013). The contrasting patterns found between small and large scale studies may be partially driven by confounding factors that co-vary with diversity, and that may also influence the invasion success, such as propagule pressure or resource availability (Levine and D'Antonio 1999; Shea and Chesson 2002, Hierro et al. 2005), which in turn influence the temporal differences between invasion stages (Clark and Johnston 2011; Clark et al. 2013). On the other side, the mechanistic Fluctuating Resources Theory (FRT, Davis et al. 2000) suggests that invasibility is also negatively related to resources' levels, so communities are more susceptible to invasion whenever there is an amount of unused resources. Therefore, community's susceptibility to invasion is not a static or permanent attribute, but a condition that can fluctuate over time.

Almost all manipulative invasibility experiments carried out so far have used small, simple model systems, mostly semi-natural or early successional grasslands (e.g., Naeem et al. 2000; Kennedy et al. 2002), as well as terrestrial (e.g., Van Ruijven et al. 2003; Fargione and Tilman 2005) or aquatic mesocosms (e.g., Stachowicz et al. 1999; Stachowicz and Byrnes 2006; Marraffini and Geller 2015). There is increasing concern regarding whether the results from these experiments can be generalized to mature systems with complex community structures, such as forests (Scherer-Lorenzen et al. 2007). However, the inherent difficulties of manipulating mature communities, due to the large experimental areas needed, and the long-term responses expected, account for the lack of invasibility experimental studies in these communities.

One aspect that deserves further investigation is whether invasibility depends more on the functional diversity than on taxonomic diversity, given that the functional structure can be far more important than species richness in determining the use of and competition for resources (Fargione et al. 2003; McGranahan et al. 2012; Maron and Marler 2008). Therefore, in mature, vertically structured communities such as forests, invasibility may be modulated by the presence of different functional groups (Arenas et al. 2006).

Shallow benthic marine communities dominated by perennial canopy algae on rocky bottoms are analogous to terrestrial forests in many aspects. They are spatially and vertically structured and species strongly compete for limiting resources, mainly space and light (Valdivia et al. 2005; Östman et al. 2016). These benthic communities, characterized by high species turnover and the small spatial scale of ecological processes, are excellent model systems for conducting manipulative experiments on invasibility relationships as examples of undisturbed complex communities (Clark and Johnston 2011).

Furthermore, in mature forest communities, whether terrestrial, freshwater or marine, epiphytes are an essential component of biological diversity, where they make up one-third to one-half of total species richness and biomass (Flores-Palacios and García-Franco 2006). Epiphytic organisms have been introduced and have invaded many ecosystems, from terrestrial forests to macroalgal kelp forests (i.e. Cebrian and Ballesteros 2010, Ladwig and Meiners 2009). As epiphyte abundance is positively related to the habitat-former species area, size or abundance (Flores-Palacios and García-Franco 2006) and frequently shows species specific relationships (Lewis and Ellis 2010), they are ideal model organisms with which to evaluate species-specific interactions (Callaway et al. 2002) that may drive invasibility dynamics in a different way that what has been described using organisms that do not share this specific trait.

In the Mediterranean Sea, canopy algae of the genus *Cystoseira* are characteristic of low-shore habitats on rocky coasts (Giaccone and Bruni 1973). *Cystoseira* species are ranked amongst the oldest erect macroalgae known to date, they have a slow dynamics with plants that can be up to 50 year old (Ballesteros et al. 2009). The multilayered vegetation associated with them makes *Cystoseira* forests morphologically comparable to mature terrestrial forests (Ballesteros et al. 2009). Thus, *Cystoseira* are important habitat formers that provide a substrate for smaller macroalgae and shelter for a wide array of benthic invertebrates (Ballesteros 1992). These seaweed forests have been invaded by several exotic algae species. One of the most abundant invaders is the red filamentous facultative epiphytic alga *Lophocladia lallemandii* (Montagne) F. Schmitz (hereafter *Lophocladia*) (Cebrian and Ballesteros 2010, Verlaque et al. 2015).

Using observational and removal experiments, we examined the susceptibility of *Cystoseira balearica* Sauvageau (hereafter *Cystoseira*) forests to invasion by *Lophocladia* and how this susceptibility changes over the stages of the invasion. Specifically, our main questions were as follows: (1) Is there a relationship between native algae species richness and *Lophocladia* invasion success? (2) Does the relationship between native algal species richness and *Lophocladia* invasion success change with the time since invasion? (3) How do functional groups contribute to the invasion success of *Lophocladia,* and (4) how do functional groups determine the relationship between native algal species richness, abundance and invasion success?

Methods

Study system

Lophocladia is a filamentous red macroalga currently spreading throughout most of the Mediterranean Sea. It was likely introduced from the Red Sea (Verlaque et al. 2015). In addition to anchoring to bare substrate, *Lophocladia* can also grow epiphytically, being a facultative epiphyte. Thus, its initial establishment does not appear to be limited by space. Due to its fast growth, *Lophocladia* can cover most types of substrate, giving the benthic seascape a homogeneous appearance (Ballesteros et al. 2007; Cebrian and Ballesteros 2010). However, the invasion of this alga is extremely patchy, with neighboring areas either heavily invaded or not invaded at all, even in areas subjected to similar propagule pressure (Cebrian and Ballesteros 2010; Marbà et al. 2014). This suggests that factors other than propagule pressure, fecundity and defense contribute to the success of the *Lophocladia* invasion.

The study was conducted in Cabrera Archipelago National Park, located in the Balearic Islands (western Mediterranean, 39°12′ 21″N; 2°58′44″E), which was established as a Marine Protected Area in 1991. *Lophocladia* was detected for the first time in Cabrera in 2003 and has spread rapidly, but patchily, over many subtidal rocky habitats (Cebrian and Ballesteros 2010).

The study was performed in well-shaped, mature *Cystoseira* forests where *Lophocladia* propagule pressure has proved to be high and homogeneous across the area (Cebrian and Ballesteros 2010). Mature *Cystoseira* forests form complex three-dimensional communities mainly dominated by canopy-forming macroalgae (approximately 20 cm tall), which harbor high biodiversity and have high productivity. However, when disturbed, *Cystoseira* forests are replaced by alternate stable states [sensu Knowlton (2004) and references therein] deprived of canopy algae and dominated by turf macroalgae or by barrens with encrusting coralline algae (Bonaviri et al. 2011).

Changes in invasion success through time and space

Throughout our study, we used *Lophocladia* abundance (as % of cover) as an estimate of invasion success because it captures population growth and is therefore a more precise measure of exotic species performance than species presence. Moreover, abundance is more closely related to spread and impact than presence (Catford et al. 2012).

Temporal survey

To assess temporal changes in *Lophocladia* abundance (% cover) and native species richness in algal forests, species surveys were conducted at the local scale at different invasion stages. Sampling was performed just after the initial invasion stage (2003) and twice afterwards (2005 and 2007). In each sampling year, six sites dominated by *Cystoseira* were randomly surveyed (separated by ca. > 500 m) by means of three 20 cm × 20 cm random quadrats from which all species were scraped. All species from each quadrat were stored in individual plastic bags and fixed with formol 10% for later species identification and quantification in the laboratory, allowing the estimation of richness and cover of native species and *Lophocladia*. Species cover was estimated by spreading specimens over a plastic tray to form a thin layer and measuring the horizontal surface area covered (in cm^2). *Lophocladia* abundance was expressed as its percentage of cover with respect to the total macroalgae cover.

Spatial survey

We also examined how patterns of *Lophocladia* abundance and native species richness changed in space by sampling across a native species richness gradient. In 2007, when the invasion was established through the Archipelago of Cabrera, a total of 60 quadrats (25 cm × 25 cm, reticulated in 5 cm × 5 cm subquadrats) were randomly sampled along 10 km of the coast dominated by *Cystoseira* forests. Both the number of native algal species and the abundance of *Lophocladia* were estimated in each quadrat. The abundance of *Lophocladia* in each quadrat was assessed by recording the number of subquadrats in which *Lophocladia* was present (Cebrian et al. 2000).

The role of functional groups in determining invasion success

We conducted a removal experiment to explore whether the invasion success of *Lophocladia* during the initial invasion stages was dependent on the functional complexity, species richness or abundance of the algal community. In a 25 m^2 patch of a mature *Cystoseira* forest not yet colonized by *Lophocladia* but with invaded areas nearby, 36 interspersed plots (25 cm × 25 cm) were established at random. Twelve randomly selected plots were left unmanipulated as controls (“CON”), harboring three algal functional groups (canopy, turf and encrusting algae); another twelve plots were manipulated by removing the canopy algae while maintaining the encrusting and turf functional groups (“ENC-TU”), whereas in the last twelve plots, both the canopy and the turf-forming algae were removed, leaving only the encrusting algae (“ENC”). The abundance (% cover) of *Lophocladia* and the abundance of every native species in each plot was assessed using reticulated (25 cm × 25 cm) quadrats, and the number of subquadrats in which each species appeared was recorded and used as unit of abundance (Cebrian et al. 2000). The mean numbers of species for each treatment was 13, 11 and 4 for CON, ENC-TU and ENC, respectively, and the species present for each treatment are detailed in Table S1. The species richness were the lowest in the ENC plots ($F_{2,33} = 63.36$; $p < 0.0001$) but not significantly different between the other two treatments. Similarly, removal of the functional groups led to a decrease on the initial native species abundance, being significantly different for all treatments ($F_{2,33} = 66{,}57$; $p < 0.0001$) and higher in the CON treatment and lower in ENC plots.

We finished the experiment 8 months after treatment when at least 20% of the quadrats were completely invaded.

Statistical analysis

In the temporal survey, differences across years as *a proxy* for different invasion stages, on the native species richness and *Lophocladia* abundance were analyzed using one-way analysis of variance (ANOVA). For the temporal and spatial surveys, the relationship between species richness and invasion success (measured as *Lophocladia* abundance) was examined using least-squares linear regressions. Differences in slopes among regression lines were explored using analysis of covariance (ANCOVA).

We first analyzed data from the removal experiment by one-way ANOVA to test for significant differences of *Lophocladia* abundance among functional group treatments. Where a significant effect of functional group was detected, Tukey's tests were used to contrast the mean values for significant differences within treatment pairs. Differences in slopes and intercepts among regressions between *Lophocladia* abundance and native species richness and abundance were preliminarily explored using ANCOVA. Finally, general linear regression models (GLMs) were used to test the influence of species richness, functional group treatments and native species abundance on *Lophocladia* abundance. We assumed a Gaussian distribution for the *Lophocladia* abundance and used a General Linear Models function with an identity link. We compared the resulting models using Akaike's Information Criterion (AICc) and Akaike weights. Data were analyzed using the statistical software R, version 2.14.2 (R Development Core Team 2011).

Results

Changes in invasion success over time and space

In the survey conducted over 3 years, site variability within each year prevented the detection of significant differences in *Lophocladia* abundance (ANOVA, $F_{2,15} = 2.612$; $p = 0.126$), although a moderate increase in percentage of cover was observed after 2 years of the invasion, and remained stable afterwards (2003: 17.73 ± 3.22; 2005: 34.72 ± 7.71; 2007: 35.85 ± 10.84; mean ± SE hereafter) (Fig. 1). In contrast, the survey revealed a progressive significant reduction (ANOVA: $F_{2,15} = 3.746$; $p = 0.048$) in species richness through time (2003: 13.83 ± 1.22; 2005: 11.33 ± 1.08; 2007: 9.50 ± 1.05).

We also observed contrasting results for the relationships between *Lophocladia* abundance and species richness (Fig. 1). The slope of the correlation between *Lophocladia* abundance and species richness significantly changed during invasion. ANCOVA model show a significant effect of species richness ($F_{1,14} = 14.870$; $p = 0.001$) and a significant interaction term between native richness ($F_{1,14} = 5.163$; $p = 0.039$). These results suggest that the slope of the regression between native richness and *Lophocladia* abundance significantly changed among years, being positive at the initial stage of the invasion (2003) but shifting to negative 2 years after invasion (2005), and remaining negative 4 years after invasion (2007) (Fig. 1). The survey across 60 sites sampled at random along 10 km of coast conducted in 2007 also revealed a significant negative correlation between *Lophocladia* abundance and species richness (Fig. 2).

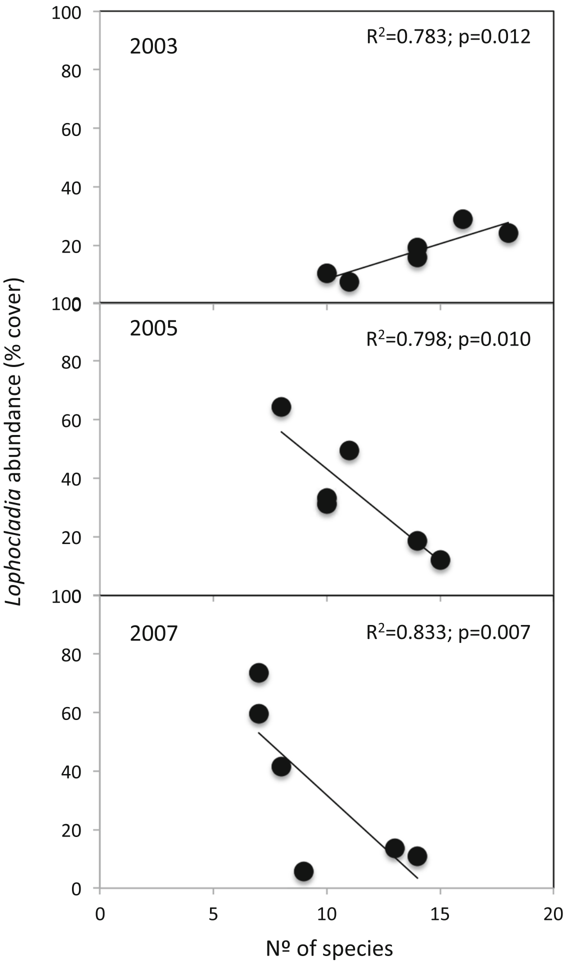

Fig. 1 Relationship between the abundance of the macroalga *Lophocladia lallemandii* and the number of native algae species at the beginning of (2003) and throughout the invasion (2005 and 2007)

The role of functional groups in determining invasion success

Lophocladia cover was highest in the CON treatment (77 ± 9.0%), was moderate in the TU-ENC treatment (61 ± 5.8) and was lowest in the ENC treatment (43.6 ± 8.6) (ANOVA: $F_{2,33} = 8.714$; $p < 0.001$). Indeed, *Lophocladia* cover was positively correlated to species richness within all functional group treatments and displayed similar slopes in all treatments (ANCOVA, $F_{2,30} = 0.833$, $p = 0.444$) (Fig. 3b). The plots with the highest *Lophocladia* cover were those displaying the highest species richness (Fig. 3c).

Similarly, *Lophocadia* cover was higher in plots were native algal species abundance was highest ($R^2 = 0.271$; $p < 0.001$). However, regarding the correlation within each functional group separately, *Lophocladia* abundance did not show any significant correlation with native algal abundance (Fig. 3b).

The best model, which explained 62% of the variation in *Lophocladia* cover, included native species richness, functional group treatment and abundance, although abundance did not show any significant effect (Table 1). Analysis of the deviance of the full GLM considering only the species richness showed that it significantly contributed to 41% of the variance explaining *Lophocladia* abundance, while functional groups alone explained no more than 34%.

Discussion

The positive relationships found between native species richness and invasion success of *Lophocladia* at the initial stages of the invasion, are consistent with Fridley et al. (2007) assertion that, at the local scale, biodiversity-invasibility relationships are not necessarily negative. In fact, communities rarely show evidence of being saturated with species because native species are not necessarily the best competitors or the most effective exploiters of their environment. Instead, native communities may leave "empty niches" available for colonization by exotic species, or they may be outcompeted by exotic species that are able to convert resources into offspring more efficiently (Fridley 2011).

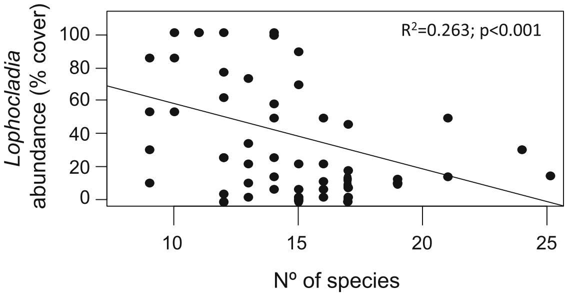

Fig. 2 Relationship between the abundance of *Lophocladia lallemandii* (% cover) and the number of native algae species across 60 sites randomly sampled along 10 km of the coast

Our results contrast with previous studies performed in early successional marine communities (e.g., Stachowicz et al. 1999; Stachowicz and Byrnes 2006; Marraffini and Geller 2015) that found that species rich assemblages were less susceptible to invasion. Although few studies manipulating species richness are available in macroalgal forests, it has been suggested that *Caulerpa cylindracea* invasion success might be higher in species-rich communities than in those with a low number of native species (Ceccherelli et al. 2002; Bulleri and Benedetti-Cecchi 2008). However, these studies reported that rather than species richness, the complexity of substrata and functional group diversity (which co-vary with species richness) were probably key factors in determining invasion success. Similarly, we found significant differences in *Lophocladia* success depending on the structural complexity of the native community, with the lowest success in the more simple communities. The processes underlying the invasions of *C. cylindracea* and *Lophocladia* may be similar. As both species can overgrow natives, higher functional complexity provides a three-dimensional spatial structure that favors the entrapment of fragments of these algae and the anchoring of their stolons (*Caulerpa*) or disk-like holdfasts (*Lophocladia*) (Ceccherelli et al. 2002; Ballesteros et al. 2007; Bulleri and Benedetti-Cecchi 2008; Cebrian and Ballesteros 2009, 2010). Our experiment shows that over all, increasing functional groups increases native algal abundance directly facilitating *Lophocladia* invasibility by providing more multiple suitable substrata for colonization (resources). However, within each functional group treatment, the lack of relationship between native species abundance and *Lophocladia* cover mean that other factors are operating at this level. Bulleri et al. (2016) recently demonstrated that in *Cystoseira* forests, long-living branches are subject to primary

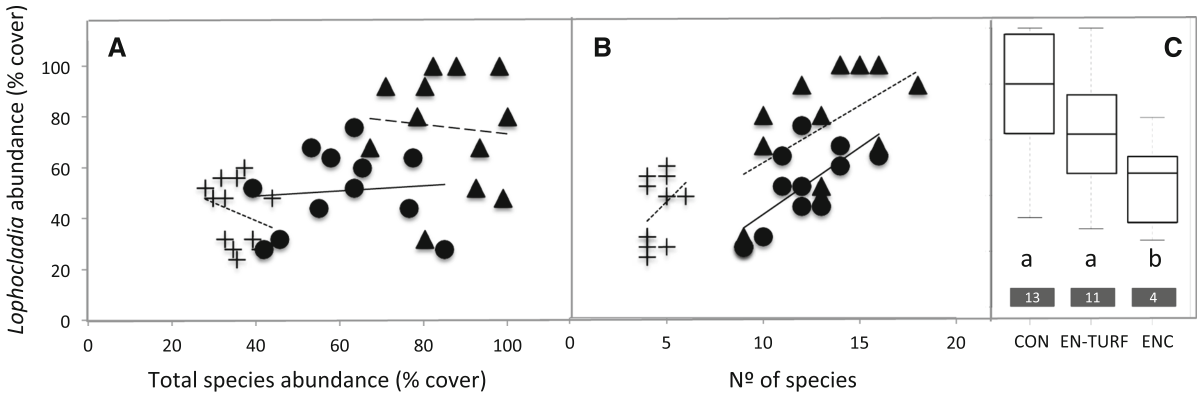

Fig. 3 Relationships between the abundance of *Lophocladia lallemandii* with native species abundance (**a**) and the species richness (**b**) for the "ENC" ($R^2 = 0.33, p < 0.05$) (···●+····), "ENC-TURF" ($R^2 = 0.396$, $p < 0.05$) (--▲-------) and "CON" ($R^2 = 0.27$, $p < 0.05$) (———) functional group treatments. (**c**) Box-plots showing the mean and CI for the abundance of *Lophocladia* in the three different functional group treatments. Values in grey quadrats indicate the mean number of species for each functional group treatment. Different lower-case letters indicate differences between groups based on Tukey's HSD test for both *Lophocladia* abundance and native algae species richness. "ENC" = encrusting, "ENC-TURF" = encrusting and turf, "CON" = unmanipulated

Table 1 Explanatory variables of the GLM for the overall experimental set-up, considering functional diversity (FG) and NSR and native abundance (n_abudance)

Variable	Factors	D2	AIC	Pr (> χ)
Lophocladia	NSR * FG * n_abundance	62.50	301.78	
	NSR			< 0.0001
	FG			0.0006
	n_abundance			0.1256

epiphyte succession processes, preventing them to be readily available for colonization (saturation of the tree, sensu Loreau 1998), discouraging the arrival of new species. This could explain that, within the CON or ENC-TU treatment, plots with higher abundance of native species (probably due to the presence of greater individuals) did not present higher abundance of *Lophocladia* (Fig. 3a). Therefore, we can conclude that at early stages of invasion, high levels of community complexity and native algal abundance (i.e., a well-developed canopy strata or a dense turf) facilitates *Lophocladia* establishment in infralittoral macroalgal-dominated communities. We also suggest that in mature complex species assemblages (considering the same habitat complexity), high species richness probably facilitates habitat invasibility by means of providing more complexity for the exotics to become established (Rejmánek 1996; Fine 2002; Stohlgren et al. 2003; Howard et al. 2005; Brooks and Jordan 2013). Then, facilitation might play an important role in the diversity-invasibility relationship as already pointed out Howard et al. (2005) and Brooks and Jordan (2013) for terrestrial ecosystems and Bulleri and Benedetti-Cecchi (2008) and Bulleri et al. (2008) for marine ecosystems. These positive relationships at the initial invasion stages can, however, become negative thorough the invasion process. We show that the positive relationship between native species richness and *Lophocladia* abundance turned to negative afterwards (Fig. 2), probably because at increasing *Lophocladia* abundance, facilitation processes become weaker at expenses of competition between natives and the invader at small scale.

All this results can be summarized with a conceptual model, which suggest that the negative relationships found in other studies between invasibility and native species richness would be that these relationships are very often studied in resource-limited communities where competition is the first structuring force (i.e., early successional grasslands and marine invertebrate-dominated communities) or once the invasion is well established in mature systems (T_{i+x}, Fig. 4). We contend that the latter negative relationships may be derived from the invasion itself. A shift in the diversity-invasibility slope will probably occur as the result of the continued negative effect of the invasive species on native communities over a long period of time, which should reduce the diversity of native species through competition. Therefore, the negative relationship between native species richness and invasibility in areas that have been invaded for a long time may be due not to the higher susceptibility of species-poor habitats to invasion (which is commonly proposed as an explanation when negative relationships are found) but to a decrease in species richness caused by the invasion, probably as a consequence of the high competitive ability of the invasive species. In line with this framework, Stohlgren et al. (2003) noted that non-positive relationships between native and invasive species richness could be expected in heavily invaded sites because exotic species could become dominant and replace native species through competition. Thus, using the relationship between invasive species abundance and species richness to assess invasibility in systems without resource limitations only makes sense when performed during the early stages of invasion (T_i, Fig. 4) because at the advanced stages what we observe is the impact of the invader on native species.

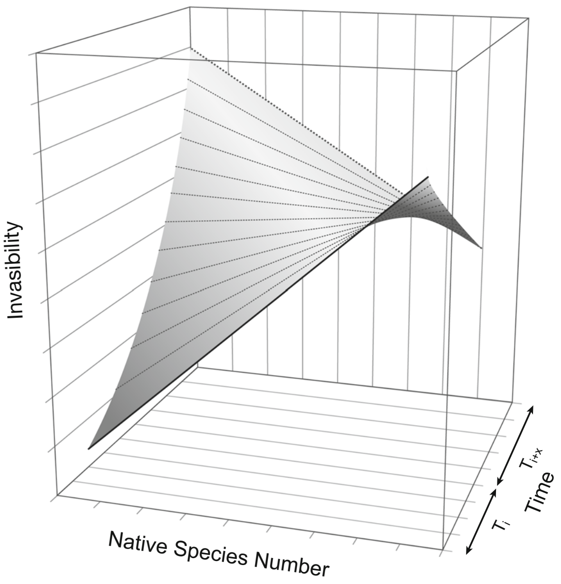

Fig. 4 Conceptual model explaining the time dependence of the biodiversity-invasibility relationships at different invasion stages. If a system is not resource limited, the relationship is initially (T_i) positive (continuous line), but at some time after the invasion (T_{i+x}), the slope shifts from positive to negative (dotted line) due to the competition of the invader. The shift from positive to negative will take less time when competition is stronger

Facultative epiphytism and the ability to grow in multiple substrates are shared by more than 75% of the most problematic invasive algae of the Mediterranean Sea (Otero et al. 2013), which are also invading the most complex and diverse habitats (e.g., *C. cylindracea*, *Womersleyella setacea* or *Acrothamnion preissii* in algal forests, coralligenous habitats or *Posidonia oceanica* meadows) (Verlaque et al. 2015). Therefore, our findings are likely to be generalizable to other communities in algal, marine and terrestrial systems invaded by species with similar traits (e.g., vines) (Ladwig and Meiners 2009).

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References

Arenas F, Sánchez I, Hawkins S, Jenkins S (2006) The invasibility of marine algal assemblages: role of functional diversity and identity. Ecology 87:2851–2861

Ballesteros E (1992) Els vegetals i la zonació litoral: espècies, comunitats i factors que influeixen en la seva distribució. Arx Secc Ciències IEC 101:1–656

Ballesteros E, Cebrian E, Alcoverro T (2007) Mortality of shoots of *Posidonia oceanica* following meadow invasion by the red alga *Lophocladia lallemandii*. Bot Mar 50:8–13

Ballesteros E, Garrabou J, Hereu B, Zabala M, Cebrian E, Sala E (2009) Deep water stands of *Cystoseira zosteroides* C. Agardh (Fucales, Ochrophyta) in the Northwestern Mediterranean: insights into assemblage structure and population dynamics. Estuar Coast Shelf Sci 82:477–484

Bonaviri C, Vega Fernández T, Fanelli G, Badalamenti F, Gianguzza P (2011) Leading role of the sea urchin *Arbacia lixula* in maintaining the barren state in southwestern Mediterranean. Mar Biol 158:2505–2513

Brooks WR, Jordan RC (2013) Propagule pressure and native species richness effects drive invasibility in tropical dry forest seedling layers. Perspect Plant Ecol Evol Syst 15:162–170

Bulleri F, Benedetti-Cecchi L (2008) Facilitation of the introduced green alga, *Caulerpa racemosa*, by resident algal turfs: experimental evaluation of underlying mechanisms. Mar Ecol Prog Ser 364:77–86

Bulleri F, Bruno JF, Benedetti-Cecchi L (2008) Beyond Competition: incorporating positive interactions between species to predict ecosystem invasibility. PLoS Biol 6(6):e162

Bulleri F, Benedetti-Cecchi L, Jaklin A, Ivesa L (2016) Linking disturbance and resistance to invasion via changes in biodiversity: a conceptual model and an experimental test on rocky reefs. Ecol Evol 6:2010–2021

Callaway RM, Reinhart KO, Moore GW, Moore DJ, Pennings SC (2002) Epiphyte host preferences and host traits: mechanisms for species-specific interactions. Oecologia 132:221–230

Capers RS, Selsky R, Bugbee GJ, White JC (2007) Aquatic plant community invasibility and scale-dependent patterns in native and invasive species richness. Ecology 88:3135–3143

Catford JA, Vesk PA, Ricardson DM, Pysek P (2012) Quantifying levels of biological invasion: towards the objective classification of invaded and invasible ecosystems. Glob Change Biol 18:44–62

Cebrian E, Ballesteros E (2009) Temporal and spatial variability in shallow- and deep-water population of the invasive *Caulerpa racemosa* var. *cylindracea* in the Western Mediterranean. Estuar Coast Shelf Sci 83:469–474

Cebrian E, Ballesteros E (2010) Invasion of Mediterranean benthic assemblages by red alga *Lophocladia lallemandii* (Montagne) F. Schmitz: depth-related temporal variability in biomass and phenology. Aquat Bot 92:81–85

Cebrian E, Ballesteros E, Canals M (2000) Shallow rocky bottom benthic assemblages as calcium carbonate producers in the Alboran Sea (Southwestern Mediterranean). Oceanol Acta 23:311–322

Ceccherelli G, Piazzi L, Balata D (2002) Spread of introduced *Caulerpa* species in macroalgal habitats. J Exp Mar Bio Ecol 280:1–11

Clark GF, Johnston EL (2011) Temporal change in the diversity–invasibility relationship in the presence of a disturbance regime. Ecol Lett 14:52–57

Clark GF, Johnston EL, Leung B (2013) Intrinsic time dependence in the diversity–invasibility relationship. Ecology 94:25–31

Davis MA, Grime JP, Thompson K (2000) Fluctuating resources in plant communities: a general theory of invasibility. J Ecol 88:528–534

Elton CS (1958) The ecology of invasions by animals and plants. Methuen, London

Fargione J, Tilman D (2005) Diversity decreases invasion via both sampling and complementarity effects. Ecol Lett 8:604–611

Fargione J, Brown CS, Tilman D (2003) Community assembly and invasion: an experimental test of neutral versus niche processes. Proc Nat Acad Sci 100:8916–8920

Fine PVA (2002) The invasibility of tropical forests by exotic plants. J Trop Ecol 18:687–705

Flores-Palacios A, García-Franco JG (2006) The relationship between tree size and epiphyte species richness: testing four different hypotheses. J Biogeogr 33:323–330

Fridley JD (2011) Invasibility of communities and ecosystems. In: Simberloff D, Rejmanek M (eds) Encyclopedia of biological invasions. University of California, Berkeley and Los Angeles, pp 356–359

Fridley JD, Stachowicz JJ, Naeem S, Sax DF, Seabloom EW, Smith MD, Stohlgren TJ, Tilman D, Von Holle B (2007) The invasion paradox: reconciling pattern and process in species invasions. Ecology 88:3–17

Giacconne G, Bruni A (1973) Le Cistoseire e la vegetazione sommersa del Mediterraneo. Atti Ist Ven Sci Lett Arti 131:59–103

Hierro JL, Maron JL, Callaway RM (2005) A biogeographical approach to plant invasions: the importance of studying exotics in their introduced and native range. J Ecol 93:5–15

Howard TG, Gurevitch J, Hyatt L, Carreiro M, Lerdau M (2005) Forest invasibility in communities in southeastern New York. Biol Invasion 6:393–410

Kennedy TA, Naeem S, Howe KM, Knops JMH (2002) Biodiversity as a barrier to ecological invasion. Nature 147:636–638

Knowlton N (2004) Multiple "stable" states and the conservation of marine ecosystems. Prog Oceanogr 60:387–396

Ladwig LM, Meiners SJ (2009) Impacts of temperate lianas on tree growth in young deciduous forests. For Ecol Manag 259:195–200

Levine JM, D'Antonio C (1999) Elton revisited: a review of evidence linking diversity and invasibility. Oikos 87:15–26

Lewis JEJ, Ellis CJ (2010) Taxon-compared with trait-based analysis of epiphytes, and the role of tree species and tree age in community composition. Plant Ecol Divers 3:203–210

Lonsdale WM (1999) Global patterns of plant invasions and the concept of invasibility. Ecology 80:1522–1536

Loreau M (1998) Biodiversity and ecosystem function: a mechanistic model. Proc Nat Acad Sci 95:5632–5636

Marbà N, Arthur R, Alcoverro T (2014) Getting turfed: the population and habitat impacts of *Lophocladia lallemandii* invasions on endemic *Posidonia oceanica* meadows. Aquat Bot 116:76–82

Maron J, Marler M (2008) Field-based competitive impacts between invaders and natives at varying resource supply. J Ecol 96:1187–1197

Marraffini ML, Geller JB (2015) Species richness and interacting factors control invasibility of a marine community. Proc R Soc B 282:20150439

McGranahan DA, Engle DM, Wilsey BJ, Fuhlendorf SD, Miller JR, Debinski DM (2012) Grazing and an invasive grass confound spatial pattern of exotic and native grassland plant species richness. Basic Appl Ecol 13:654–662

Naeem S, Knops JMH, Tilman D, Howe KM, Kennedy T, Gale S (2000) Plant diversity increases resistance to invasion in the absence of covarying extrinsic factors. Oikos 91:97–108

Östman Ö, Eklöf J, Eriksson BK, Olsson J, Moksnes PO, Bergstrom U (2016) Top-down control as important as nutrient enrichment for eutrophication effects in North Atlantic coastal ecosystems. J Appl Ecol 53:1138–1147

Otero M, Cebrian E, Francour P, Galil B, Savini D (2013) Monitoring marine invasive species in Mediterranean Marine Protected Areas (MPAs): a strategy and practical guide for managers. IUCN, Malaga, p 136

R Development Core Team (2011) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Rejmánek M (1996) Species richness and resistance to invasions. In: Orians G, Dirzo R, Cushman H (eds) Biodiversity and ecosystem processes in tropical forests. Springer, Berlin, pp 153–172

Robinson GR, Quinn JF, Stanton ML (1995) Invasibility of experimental habitat islands in a California winter annual grassland. Ecology 76:786–794

Scherer-Lorenzen M, Schulze ED, Don A, Schumacher J, Weller E (2007) Exploring the functional significance of forest diversity: a new long-term experiment with temperate tree species (BIOTREE). Perspect Plant Ecol Evol Syst 9:53–70

Shea K, Chesson P (2002) Community ecology theory as a framework for biological invasions. Trends Ecol Evol 17:170–176

Simberloff D (2009) The role of propagule pressure. Ann Rev Ecol Evol Syst 40:81–102

Stachowicz JJ, Byrnes JE (2006) Species diversity, invasion success, and ecosystem functioning: disentangling the influence of resource competition, facilitation, and extrinsic factors. Mar Ecol Prog Ser 311:251–262

Stachowicz JJ, Whitlatch RB, Osman RW (1999) Species diversity and invasion resistance in a marine ecosystem. Science 286:1577–1579

Stohlgren TJ, Barnett DT, Kartesz JT (2003) The rich get richer: patterns of plant invasions in the United States. Front Ecol Environ 1:11–14

Theoharides KA, Dukes JS (2007) Plant invasion across space and time: factors affecting nonindigenous species success during four stages of invasion. New Phytol 176:256–273

Valdivia N, Heidemann A, Thiel M, Molis M, Wahl M (2005) Effects of disturbance on the diversity of hard-bottom macrobenthic communities on the coast of Chile. Mar Ecol Prog Ser 299:45–54

Van Ruijven J, De Deyn GB, Berendse F (2003) Diversity reduces invasibility in experimental plant communities: the role of plant species. Ecol Lett 6:910–918

Verlaque M, Ruitton S, Mineur F, Boudouresque CF (2015) CIESM Atlas of exotic species in the Mediterranean. In: Briand F (ed) Macrophytes, vol 4. CIESM, Monaco, p 364

Vilà M, Pino J, Font X (2007) Regional assessment of plant invasions across different habitat types. J Veget Sci 18:35–42