Donor-Recipient Relationships of Non-Indigenous Marine Macroalgae between Tropical Pacific Islands

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Abstract – The Pacific Island region is an ideal setting for case studies on the invasion history of macroalgae in tropical coastal waters. Many textbook examples of algal invasions in this region demonstrate their significant ecological impacts on native reef communities. In light of increased maritime traffic as a potential anthropogenic dispersal mechanism for non-indigenous marine algae between tropical North Pacific Islands, a risk assessment was conducted to (1) quantify floristic disparities between marine ecoregions based on three subsets of species inventories, (2) evaluate the environmental and spatial distribution characteristics of island floras that are conducive to new introductions, and (3) establish a baseline with which future risk assessments based on a molecularly-assisted alpha taxonomy concept may be compared. The results of the environmental and floristic analyses showed that the “potentially invasive species” (i.e., species belonging to genera with known invasive representatives) constitute the best taxonomic subset for future risk assessments of marine macroalgae as this group (1) consists of an adequate—yet manageable—number of species, (2) is characterized by environmental and distribution parameters similar to that of the entire flora, (3) alleviates the deficit of non-indigenous species detection in tropical waters due to a historical bias toward temperate waters, and (4) closely mimics proportional differences in species composition between entire floras.

Algae / Caroline Islands / Chuuk / Hawaiian Islands / Mariana Islands / Federated States of Micronesia / Guam / Pohnpei / Invasive Species Risk Assessment / Non-Indigenous Marine Species / NIMS / Okinawa / Palau / Regional Biosecurity Plan / Ryukyu Islands / Seaweed / Yap

INTRODUCTION

The study of non-indigenous marine species (NIMS) is a field that arose when newly introduced NIMS were observed to invade native biological communities often resulting in significant economic and environmental costs. Most of the initial studies focused on temperate regions. Through globalization and shifting economic power, the introduction and outbreaks of NIMS are now a major global concern. The number of studies on the history, ecology and economic impact of NIMS introductions, however, still show a latitudinal bias toward temperate waters (Lowry et al., 2013) because baseline diversity assessments are incomplete or lacking for many (sub)tropical shores, an issue that is compounded

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by the higher degree of biodiversity in the tropics. Globally, marine macroalgae make up about 20% of all NIMS (Andreakis & Schaffelke, 2012). The tropical North Pacific region is replete with textbook examples of non-indigenous marine macroalgae for which the introduction and invasion history is well-documented. The ecological and economic impacts of these introductions have also been studied in detail for some of the larger and economically important islands like the Main Hawaiian Islands (Lovell et al., 2006), where they acted as drivers of ecosystem change rather than passengers or back-seat drivers (Bauer, 2012). The rhodophyte *Acanthophora spicifera* (M.Vahl) Børgeisen is probably the best known algal invader with considerable adverse impacts on the marine ecosystems of the region. The alga was introduced to Pearl Harbor in the early 1950’s, probably by a heavily fouled barge originating from Guam (Doty, 1961). After settlement in Pearl Harbor, it quickly spread around Oahu and all other Hawaiian Islands and is now the most abundant alien alga in the Hawaiian Islands displacing native macroalgae (Smith et al., 2002). The species continues to invade new islands in the Central Pacific and was recently recorded for the first time in the Marshall Islands (Tsuda et al., 2008) and the Line Islands (Knapp et al., 2011). The study of donor-recipient relationships of NIMS in the tropical Pacific is particularly topical as the marine invasion risk assessment of the regional biosecurity plan for Micronesia and Hawai’i (Hewitt et al., 2015) requires validation and improvement (University of Guam Regional Biosecurity Plan Development Team, 2105). The present study follows the morphospecies (Ruse, 1969; Krell, 2004) approach of the regional biosecurity plan as (1) this allows for the inclusion of the reported spatial distribution and environmental ranges of macroalgal species in the analysis and (2) the discovered relationships will serve as a baseline to compare with future risk analyses in the region based on molecular operational taxonomic units (MOTUs; Blaxter, 2004). More specifically, the present study investigates the potential exchange of non-indigenous macroalgae between six marine ecoregions in the tropical North Pacific as (1) maritime traffic between these islands is expected to increase in light of the military realignment in the Asia-Pacific region (Marler et al., 2012), (2) this island region is prone to introductions as the natural dispersal capacity of algae to these distant island groups is low (Kinlan & Gaines, 2003) because of the vast intermittent ocean barrier that separates them, (3) historically, the macroalgal floras of these islands have been well-studied, and (4) these islands can serve as a model for marine invasive species risk assessments in other tropical regions.

In comparing floristic differences between marine ecoregions, three approaches to quantify the risk of NIMS introductions will be tested: comparisons between (1) complete floras, (2) potentially invasive species (*i.e.*, species belonging to genera of which invasive representatives have been documented), and (3) known invasive species. The first approach relies on exhaustive and very complete species distribution datasets, frequently not available in the tropics. The second approach allows resource managers to focus and compile species distribution data for a subset of the complete flora, whereas the third approach is restricted to macroalgal species that have been documented to invade new—often temperate—areas. Differences in the floristic composition of marine ecoregions based on these three floristic datasets will be examined by a correlation analysis and by comparing sea surface temperature and distribution characteristics of its composing species. These analyses will identify the main source and recipient island groups for the spread of non-indigenous marine algae in the tropical North Pacific and will provide recommendations for conducting risk assessments of non-indigenous
marine macroalgae in other tropical regions. Our study will also serve as a baseline risk assessment of non-indigenous algal morphospecies in the tropical North Pacific for comparisons with forthcoming molecular studies. This is a topical approach as cryptic diversity is known to be very high in marine macroalgae (Payo et al., 2013) but taxon identifications based on sequence analysis do not yet allow for similarity analyses of entire floras as the distribution data of such MOTUs or phylospecies is largely incomplete (Sherwood, 2008).

Due to the continuous nature of invasion risks once pathways are established and because of the significant impact of stochastic inoculation events (Carlton, 1996) related to increased maritime traffic and large-scale in-water construction and dredging activities in light of the Asia-Pacific military realignment plans, this study focuses on the potential of NIMS exchange between islands in the tropical North Pacific. Our study region is close to the hotspots of marine bioinvasions (Seebens et al., 2013), but the investigated islands are not on the main shipping lanes and maritime traffic data within the region are incomplete (Ruiz & Zabin, 2005). The unpredictability of introduction events has been underscored in a phylodirgraphic study of the rhodophyte *Asparagopsis taxiformis* (Delile) Trevisan de Saint-Léon in the Hawaiian Islands. The supposedly native Hawaiian population of this alga was augmented by two separate (cryptic) introductions of the same species from distant geographic source populations and the most recently arrived lineage is currently restricted to the south shore of the most developed island Oahu (Sherwood, 2008; Dijoux et al., 2014).

Other detailed molecular studies on macroalgae demonstrate the limited predictive power of information on past NIMS records and shipping trajectories between donor and recipient areas to reveal accurate invasion histories and patterns (Provan et al., 2005; Provan et al., 2007; Mineur et al., 2010). The present study aims to identify the total number of species that could potentially be exchanged between islands in the study region independent of a timeframe, which is the reason why maritime traffic intensity is not considered as a variable here. Our study is neither focused on assessing the vulnerability to invasions of specific habitats and communities of these Pacific Islands, but compares florals between marine ecoregions. At this broad geographical scale, the invasion paradox theory suggests a positive relationship between native and non-indigenous species richness, although greater biotic resistance might occur in tropical diversity hotspots (Fridley et al., 2007). Since the study area in the Western Pacific is just outside (1) the Indo-Malay-Philippine biodiversity hotspot (Gaither & Rocha, 2013) and (2) the Japanese hotspot of macroalgal diversity (Kerswell, 2006), the effect of species richness on biotic resistance is unclear and therefore biotic resistance was omitted as a factor in calculating the potential for NIMS introductions. The addition of biological interactions (e.g., biotic resistance) to modeling invasion risks goes beyond basic biodiversity metrics and recent theories emphasize the importance of facilitative relationships and enemy release mechanisms (Vaz-Pinto et al., 2014). Such detailed biological data are not yet available for the study region. Also, providing estimates for the positive or negative impact of non-indigenous species at large geographical scales often involves some level of subjective assessment (Sax & Gaines, 2003; Brown & Sax, 2004; Brown & Sax, 2005), the reason why this study also evaluates the risk based on all possible NIMS introductions instead of just restricting the assessment to species previously labeled as “invasive”. 
MATERIALS AND METHODS

Algal Distribution Records and Algal Groups

Comprehensive checklists of macroalgal occurrences in each of the six marine ecoregions (Spalding et al., 2007) were compiled based on literature data available in AlgaeBase (Guiry & Guiry, 2013) and regional macroalgal diversity publications. All published records were assigned to ecoregions after the inspection of detailed distribution records in the literature. Checklists were taxonomically updated through the synonymy listings in AlgaeBase. Next, global distribution ranges of the 1,260 algal species reported for the tropical North Pacific were compiled using AlgaeBase records and its source publications. Histograms representing the floristic richness of the six marine ecoregions were plotted on a three dimensional map using the keyhole markup language (KML). KML files were produced with the R2G2 package in R (R Development Core Team, 2015) and visualized in ESRI ArcGlobe 10.0.

Three categories of algae were used in the floristic analysis: (1) all marine macroalgae recorded for the six ecoregions, (2) potentially invasive species—defined as all species belonging to genera for which invasive representatives have been reported in the literature—, and (3) a subset of known invasive species. For this purpose a list of invasive macroalgae was compiled based on a baseline invasive species database derived from 350 databases and other sources (Molnar et al., 2008), with additional records of invasive macroalgae from other publications Change order as follows: (Stegenga & Prud’homme van Reine, 1998; Sapp, 1999; Renoncourt & Meinesz, 2002; Zenetos et al., 2005; Huisman et al., 2008; Sherwood, 2008; Daisie, 2009; Lyons & Scheibling, 2009; Seekbach & Chapman, 2010; Nejrup & Pedersen, 2012; Nobanis - European Network on Invasive Species, 2015; Puttock et al., 2015; Verlaque, 2015). The distribution records of these algae are available from the first author upon request. Pairwise floristic comparisons of the three algal categories between donor and recipient ecoregions were generated in Wolfram Mathematica 9. Because of (1) the relatively close proximity of the studied ecoregions, (2) the fact that many of the shipping trajectories are within the region, and (3) the absence of reliable maritime traffic data for Micronesian Islands (Hewitt et al., 2015), the net difference in floristic composition between source and sink ecoregions was used to determine risks of introducing new algal species into the six ecoregions. This approach was based on the assumption that within the study region, all algae have an equal probability of reaching other island groups.

Sea Surface Temperatures and Coastline Lengths

Environmental matching between donor and recipient regions regulates the establishment success and subsequent invasion impact of NIMS (Ricciardi et al., 2013; Iacarella et al., 2015). Water temperature is the most important environmental variable that determines macroalgal distribution ranges (Breeman, 1988; Schils & Wilson, 2006). Four sea surface temperature (SST) variables were obtained from Bio-Oracle (Tyberghen et al., 2012) to characterize the environmental tolerances of the 1,260 macroalgal species: minimum SST, average SST, maximum SST, and range in SST. SST variables were extracted from Bio-Oracle for strips of coastal waters (up to 10 km offshore) within the predefined marine ecoregions (Spalding et al., 2007) and calculated as described in Schils & Wilson (2006). The same SST variables were then computed for the entire distribution range of each species of
macroalgae and they represent the floristically-derived SST (hereafter SST<sub>fd</sub>) variables as in Schils & Wilson (2006). Total coastline length was calculated for each marine ecoregion based on the Seamless Digital Chart of The World (Version 3.2), which was then used to compute the spatial distribution of the studied species. Geographic analyses were conducted in ESRI ArcMap v10.0. Boxplots, non-parametric significance tests and correlation analyses of these variables between marine ecoregions and algal groups were performed in R (R Development Core Team, 2015), employing the packages agricolae, car, Hmisc, nortest, pgirmess, psych, reshape and the non-packaged R function anova.lm.R (http://www.bio.umontreal.ca/legendre/indexEn.html). All results were expressed as mean ± SD.

RESULTS

Patterns in Species Richness

The four marine ecoregions of Micronesia <i>sensu lato</i> were characterized by a lower species richness in comparison to the two ecoregions at the longitudinal extremes of the study area (Fig. 1). Species richness of marine ecoregions was significantly correlated with the total coastline length of landmasses within these ecoregions ($r = 0.92$, $P = 0.009$). Red algae were the most species-rich group of macroalgae for each of the marine ecoregions. The South Kuroshio ecoregion, which includes Okinawa Island, had the highest total number of algal records and the richest red, green, and brown algal florals of all six ecoregions. The East and West Caroline Islands had the lowest recorded number of algal species (316 spp. each), with the East Carolines having slightly more records of red algae and the West Carolines more greens. The high species richness of the Hawaiian Islands was primarily a result of its diverse and well-documented red algal flora.

![Fig. 1. Marine macroalgal species richness of ecoregions in the tropical North Pacific. Contours of marine ecoregions (Spalding <i>et al.</i>, 2007): South Kuroshio, Marine Ecoregion 121; Mariana Islands, Marine Ecoregion 123; East Caroline Islands, Marine Ecoregion 124; West Caroline Islands, Marine Ecoregion 125; Hawaii, Marine Ecoregion 152; Marshall Islands, Marine Ecoregion 153. Histograms represent the number of marine algal species recorded for each ecoregion with rhodophytes in red, chlorophytes in green, and ochrophytes in brown.](image)
SST$_{fd}$ and Spatial Distribution of Macroalgal Floras

Fig. 2 shows the minimum SST$_{fd}$, average SST$_{fd}$, maximum SST$_{fd}$, range in SST$_{fd}$, and total coastline length of the global distribution range for each species known from an ecoregion. Two ecoregions, the South Kuroshio and Hawaiian Islands, contained a flora of which the constituent species had a slightly—but statistically significant—lower maximum SST$_{fd}$ (30.7 ± 1.2°C and 30.3 ± 1.8°C) and average SST$_{fd}$ (24.1 ± 2.9°C and 24.6 ± 2.4°C) than the four Micronesian island groups. The flora of the South Kuroshio ecoregion was also characterized by a large number of species of which the distribution range extended into cooler waters (minimum SST$_{fd}$: 10.6 ± 7.8°C), making this the most eurythermal flora (range in SST$_{fd}$: 14.1 ± 5.5°C) of the six marine ecoregions. The global distribution range of species reported for the Caroline and Marshall Islands is significantly larger (191,128 ± 184,082 km; 178,068 ± 172,411 km; 182,598 ± 185,308 km) than those of the South Kuroshio (151,952 ± 177,324 km) and the Hawaiian Islands, the latter ecoregion being characterized by the most narrow average distribution range of macroalgal species (147,687 ± 190,296 km).
Three of the five floristically-derived environmental variables showed a significant correlation with the same physical variables that characterize each of the six ecoregions. The maximum and average SST$_{fd}$ values of the ecoregions derived from their algal floras and those measured directly from satellite imagery displayed high and significant correlations ($r = 0.92$, $P = 0.008$; $r = 0.89$, $P = 0.017$). Surprisingly, the coastline length distribution of species from these ecoregions showed an inverse correlation with the total coastline length of that ecoregion ($r = -0.82$, $P = 0.043$). Minimum SST$_{fd}$ and range in SST$_{fd}$ were not correlated with the same SST values derived from satellite imagery for the six ecoregions ($r = 0.41$, $P = 0.417$; $r = 0.48$, $P = 0.339$).

SST$_{fd}$ and Spatial Distribution of Algal Groups

The number of macroalgae in the category “known invasive species” is small (93 spp.) compared to the category of “potentially invasive species” (596 spp.) and the total macroalgal species richness of the region (1,260 spp.). The SST$_{fd}$

![Graph showing SST and coastline length for different algal groups](image)

Fig. 3. Floristically-derived sea surface temperature (SST$_{fd}$) variables and global distribution range of tropical North Pacific macroalgae categorized in three floristic subsets. Macroalgae reported for the six marine ecoregions (Figs 1-2) were grouped as follows: (1) a group encompassing all known macroalgal species from the six ecoregions, (2) a subset of the first group consisting of potentially invasive species (i.e., species belonging to genera with known invasive representatives), and (3) a more restrictive subset solely composed of known invasive species (i.e., algae previously reported to be invasive somewhere in the world). Box plot specifications as in Fig. 2.
characteristics of the “known invasive species” category differ significantly ($P < 0.001$) from the other two categories and were typified by a higher maximum SST$_{fd}$ (31.7 ± 1.3°C versus 30.5 ± 1.5°C and 30.3 ± 1.5°C), lower minimum SST$_{fd}$ (4.9 ± 5.9°C versus 12.0 ± 8.5°C and 12.9 ± 8.3°C), lower average SST$_{fd}$ (22.9 ± 3.1°C versus 24.2 ± 3.0°C and 24.5 ± 2.9°C) and higher range in SST$_{fd}$ (17.8 ± 3.8°C versus 12.6 ± 6.2°C and 11.9 ± 6.2°C; Fig. 3). The total linear coastal distribution range of its composing species was on average about 2.4-2.8 times greater than the taxa belonging to the other two algal categories (338,485 ± 249,930 km versus 139,434 ± 188,079 km and 122,139 ± 164,879 km). SST$_{fd}$ characteristics and the global distribution range of the “potentially invasive species” category did not differ significantly from those of the total flora of the region.

**Donor and Recipient Ecoregions of Marine Macroalgae**

Pairwise comparisons in species occurrences between marine ecoregions showed that the South Kuroshio and Hawaiian Islands ecoregions outweighed the other four Micronesian ecoregions in the total number of species, potentially invasive species, and known invasives (Fig. 4). In each of the three cases the highest number of non-shared species between two ecoregions always identified the South Kuroshio and Hawaiian Islands as the donor region. Donor-recipient relationships of ecoregions are most similar between an analysis of the complete flora and one based on potentially invasive species ($r = 0.99, P < 0.001$). In both cases, the South Kuroshio ecoregion was the donor in the five most different comparisons and the Hawaiian Islands were the donor region in the next five highest floristic discrepancies. Donor-recipient relationships based on an analysis of just the known invasive species showed a reorganization of the invasion threat between the ten most different ecoregion pairs, with the Hawaiian Islands being the donor region of the most different pairwise comparison between ecoregions (38 invasive macroalgae reported for the Hawaiian Islands and unknown for the East Caroline Islands). The correlation

![Image](image-url)
of donor-recipient relationships between the “known invasive species” analysis and those of the whole flora \((r = 0.91, P < 0.001)\) or just the potentially invasive species \((r = 0.93, P < 0.001)\) is statistically significant but lower than between the latter two \((r = 0.99, P < 0.001)\).

**DISCUSSION**

**Taxonomic and Environmental Characterization of Marine Ecoregions**

The significant, positive correlation between the species richness of marine ecoregions and their total shoreline lengths corresponds to the finding that the amount of available habitat (reef extent) and habitat diversity are the main variables that best explain macroalgal diversity in the Pacific Islands (Schils \textit{et al.}, 2013). The latter study also found that the composition of macroalgal communities in the tropical Pacific differs markedly between archipelagos. These reported differences in alpha diversity and community composition between tropical Pacific Islands are reflected in the donor-recipient relationships of NIMS between Pacific Island floras. The six marine ecoregions considered here are all tropical, with the South Kuroshio and Hawaiian Islands ecoregions being characterized by slightly cooler maximum and average sea surface temperatures (0.4-0.9°C colder maximum SSTs; 0.7-1.8°C colder average SSTs). Similar differences in sea surface temperature were found when analyzing the temperature affinity of the constituent macroalgal floras (\(\text{SST}_{64}\)) of these ecoregions. The global distribution range of macroalgal species from the six ecoregions, however, was inversely related to the total coastline length of these ecoregions. The average global distribution ranges of macroalgae from the two largest and most species-rich ecoregions were more restricted than those of the four smaller Micronesian ecoregions. The Hawaiian Islands were characterized by the most geographically restricted flora, probably a result of the relatively high degree of endemism in its macroalgal flora (Sherwood \textit{et al.}, 2010) due to the long evolutionary isolation of these islands (Haurigan & Reese, 1987; Fautin \textit{et al.}, 2010). As such, the Hawaiian Islands are an example of the hypothesis that the ecological impact of NIMS is greatest on islands where (1) high numbers of NIMS have successfully settled and (2) the degree of species endemism in the native fauna is high (Walsh \textit{et al.}, 2012). Past introductions of non-indigenous marine macroalgae in the Hawaiian Islands have radically altered many of the islands’ reef communities analogous to the decrease in fish diversity in the eastern Mediterranean Sea due to the arrival of Lessonian migrants (Edelist \textit{et al.}, 2013).

The high algal richness of the South Kuroshio ecoregion (classified in its own province) is consistent with the fact that the Japanese Archipelago is a hotspot of macroalgal diversity (Bolton, 1994) and has been an important donor region of invasive macroalgae (Ruines, 1989). The finding that the main risk of invasions is directed from the two largest and most species-rich island areas—even when only considering the most restricted subset of known invasive species—is consistent with the principle of limiting similarity, which assumes that the degree of niche occupation of native species defines susceptibility to invasions (Price & Pärtel, 2013). Invasion risk was highest for the Caroline Islands and the Marshall Islands, two island groups that form an important dispersal/migration corridor and connect populations of marine organisms from the Western and Central Pacific (Davies \textit{et al.}, 2015).
Consistent with the latter study, the available species inventories suggest that the tropical marine floras of the Micronesian Islands contain species that have been reported for more ecoregions and have a larger coastline distribution range than the floras of the Hawaiian Islands and the South Kuroshio ecoregions. Current biogeographical descriptors of the Micronesian flora (degree of endemism, spatial distribution, etc.) are, however, expected to change considerably if more molecularly-assisted alpha taxonomic (MAAT) studies were to focus on the macroalgae of this scientifically underserved region.

The Central Indo-Pacific Province (Spalding et al., 2007), which includes the ecoregions examined here except for the Marshall and Hawaiian Islands, has been classified as one of the most endangered marine ecosystems globally because of its high invasion risk with high evenness (Seebens et al., 2013). Here we found, however, that this marine province contains ecoregions with disparate donor-recipient characteristics of NIMS introductions. Hence, studies of invasion risk at low geographic resolution (province-level) might smoothen out or completely obscure important donor-recipient relationships of NIMS at smaller geographical scales, making small, isolated and biodiverse islands likely casualties of inaccurate invasive species risk assessments. The “Pacific Pivot” to rebalance US military forces in the Asia-Pacific region is expected to increase maritime traffic between bases in the South Kuroshio province and islands in the Tropical Northwestern Pacific province. Intensified use of connectivity pathways between one of the world’s main donor regions of invasive macroalgae and the small, geographically isolated Micronesian Islands increases the—predominantly—unidirectional risk of new introductions to these relatively pristine islands. Environmental constraints (e.g., SST thresholds) that affect the physiology of species and biotic resistance through competition with native species are natural barriers that lower the success of new arrivals but the large overlap in environmental requirements between macroalgae from these tropical Pacific Islands suggest that the majority of marine macroalgae could be exchanged between the studied ecoregions.

**NIMS Risk Assessments in the Tropics**

Risk assessments traditionally focus on known invasive species, but this approach is undesirable for tropical regions because most NIMS research efforts have been focused on temperate waters at higher latitudes, which was reflected in the significantly lower minimum, average and maximum SST$_{ld}$ affinities of this subset in comparison to those of the entire flora and the subset of potentially invasive species. This effect was compounded by similar discrepancies in research effort between ecoregions in the tropical Pacific, with a rich history of research on invasive macroalgae in the Hawaiian Islands (characterized by lower SSTs) and a paucity of such studies elsewhere in the tropical Pacific. The category of known invasive macroalgae was also characterized by an exceptionally large SST$_{ld}$ range (17.8 ± 3.8°C) throughout its global distribution range and it is contentious whether such species actually exist since high degrees of cryptic diversity have become the norm in MAAT studies of macroalgae, with species generally having much smaller distribution ranges than previously believed (Payo et al., 2013).

As the environmental characteristics of known invasive macroalgae differ significantly from those of the tropical Pacific floras for which these invasive species have been reported, they probably represent an incomplete taxonomic subset on which risk assessments should not be based. The environmental characteristics of
the group of potentially invasive species, however, are not statistically different from the macroalgal flora they are a subset of. Yet, this group of potentially invasive species contains less than half the number of species of the entire flora and are thus the subset of choice for risk assessments where the assembly of complete taxonomic lists is scientifically or economically unfeasible.

The group of known invasive species was characterized by significantly broader global distribution ranges than those of potentially invasive species or the entire macroalgal flora of the studied tropical Pacific Islands. This finding is consistent with a trait assessment of invasive macroalgae in Europe (Nyberg & Wallentinus, 2005) but is not consistent with the results of a similar assessment on a global scale (Williams & Smith, 2007), where macroalgae native to a single biogeographic region were responsible for the highest count of new introductions. The geographical analysis presented here is based on a more complete dataset using a higher degree of geographical resolution (232 marine ecoregions versus 25 and 20 biogeographical regions; Nyberg & Wallentinus, 2005; Williams & Smith, 2007), suggesting that invasive macroalgae in both tropical and temperate waters are characterized by a broader distribution range than non-invasive species.

Based on the clearly unbalanced donor-recipient relationships of NIMS in the tropical Pacific region, the precautionary principle to prevent any new introductions should be the recommended approach. The analyses demonstrated that the precautionary principle is best adhered to if future risk assessments are based on at least the potentially invasive species, which is a subset but a good surrogate of the total floristic composition of the region allowing for a compilation of environmental as well as physiological data for the these macroalgae throughout their distribution range.

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