Biol Invasions (2025) 27:148
https://doi.org/10.1007/s10530-025-03600-w

ORIGINAL PAPER

Non-native ecologically successful algae in the Hawaiian archipelago have highly competitive traits but low functional diversity

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Received: 30 August 2024 / Accepted: 30 April 2025 / Published online: 7 June 2025

Abstract The introduction of non-native algae becoming invasive is a driver of ecosystem change in many coastal areas, and understanding the ecological consequences of these introductions is important. Here we use a trait-based approach to demonstrate potential differences between native and invasive algal communities. A set of functional traits was applied to the most commonly occurring native and invasive algal species. We included the recently discovered alga *Chondria tumulosa* A.R. Sherwood & Huisman (2020) to predict its potential invasiveness on the local algal assemblages. The results indicate that invasive macroalgae have introduced certain novel functional traits to algal communities in the Main Hawaiian Islands. These algae occupy and share a specific part of the trait space, which has two key implications, either that invasive algae can alter the functional composition of local assemblages by introducing new trait values and outcompete the native flora, or, if their traits differ from those of native species, invaders might occupy habitats or utilize resources in a way that instead complement native species. An evaluation of *C. tumulosa* showed that this species has a high potential of becoming invasive and causing declines in the functional diversity of coastal habitats. Moreover, this study illustrates that trait-based analysis can provide a useful tool for evaluating the invasive potential of algal species and increasing understanding of ecological consequences of such invasions.

Keywords Macroalgae · Algal blooms · Functional diversity · Invasive algal species · Habitat effects · Macroalgal communities

Introduction

Interactions among species underpin the ecological functions of a system and subsequently its provision of ecosystem services (Mouillot et al. 2013; Mauffrey et al. 2020). These interactions are strongly linked to the functional role of a species, which is dictated by its traits—that species' morphological, behavioral and phenological characteristics (Violle et al. 2007; Cappelatti et al. 2020; Mammola et al. 2021). In

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10530-025-03600-w.

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short, a species' traits and its responses to abiotic and biotic factors determine functional roles in ecological communities and shape ecosystem functions (Cadotte et al. 2015). Viewing a system through the lens of trait-based ecology can provide strong insights into the relationships between community structure and ecosystem functioning (Díaz and Cabido 2001). Several studies of terrestrial plant communities indicate that the explanatory power of functional diversity is greater than species diversity in explaining ecosystem processes (Díaz and Cabido 2001; Mokany et al. 2008; Cadotte et al. 2011). Within terrestrial plant communities, trait-based ecology has proven useful in predicting community responses to disturbances such as introductions of invasive species (Drenovsky et al. 2012; Kunstler et al. 2016; Mathakutha et al. 2019; Palma et al. 2021; Kaushik et al. 2022). Compared to terrestrial ecology, trait-based studies are not as commonly applied to marine systems. The number of studies has increased substantially during the two last decades, but mainly for fish (Halpern and Floeter 2008; D'agata et al. 2014; Bellwood et al. 2019; Mihalitsis and Bellwood 2019), while similar studies remain scarce for algae (but see e.g., Mauffrey et al. 2020; Fong et al. 2023).

Within coral reef ecology, macroalgae are commonly described based on growth form (Littler and Littler 1980), and there is generally a lack of species-specific or functional-group resolution based on other traits. For example, the growth form described as "fleshy macroalgae" or its equivalent is usually an indicator of degraded reef health, irrespective of traits such as native or non-native status, growth rates, substrate preferences and palatability, which all can contribute to competitive success and ecosystem functions. In contrast, by describing ecological strategies of a species by using functional diversity it is possible to adopt a multidimensional perspective which is highly relevant considering the complexity and heterogeneity of marine macroalgae (Fong et al. 2023). Moreover, separating the impact of a single species on an ecological community is challenging, but by choosing ecologically relevant traits based on literature and analyzing differences in functionality among communities, this species- based understanding is possible.

Though introductions can constitute a negligible change in overall species diversity, the recipient community may experience outsized impacts on functional diversity if the invader possesses novel traits (Díaz and Cabido 2001; Pyšek et al. 2020) and/or becomes very abundant (Kaushik et al. 2022). Potential consequences of invasions include loss of functional diversity, but there is also a possibility that invasive species could add new ecological functions, especially in species-poor locations (Karlson et al. 2024). Furthermore, the functional traits of a species can contribute to an invader's success by contrasting strategies, although invasion success is also context dependent (Drenovsky et al. 2012; Mouillot et al. 2013; Kaushik et al. 2022). In order to predict the success of invasive species, several approaches and hypotheses are applied. One such hypothesis is the Darwin naturalization conundrum which explores how invasive species might either compliment or compete with native species based on trait differences and phylogenetic similarity (Marx et al. 2016; Cadotte et al. 2018). For example, non-native species may have functional traits that differ from those of native communities, allowing the invader to exploit an empty niche (Funk et al. 2008; Karlson et al. 2024). Alternatively, the invader may possess similar traits to the species already present, but also have the ability to monopolize resources and consequently outcompete and smother native flora and fauna (Franzén 2004; Funk et al. 2008; Mouillot et al. 2013; Karlson et al. 2024). The success of a marine invader will be further impacted by environmental filters (e.g. tolerance of salinity and turbidity), which can vary substantially among geographical locations (Blackburn et al. 2011; Jungblut et al. 2018). Therefore, a species that is invasive in one location may not always be problematic in another, making it difficult to predict negative effects of any one invader in a new ecosystem (Kaushik et al. 2022).

To estimate invasion potential of any particular algal species, Nyberg and Wallentinus (2005), suggested a functional traits approach. They could show that many invasive species shared certain traits for successful establishment, dispersal and spread, such as the ability to reproduce both sexually and asexually, a large thallus size and generalist substrate preferences, although this was not true across all algal groups (Nyberg and Wallentinus 2005; Littler and Littler 1980). However, these results were identified without considering existing traits of native communities, thus limiting the effectiveness of this early contribution. Clearly, an important aspect of predicting effects of invasions is examining the functional traits of the invasive species in relation to the native flora and how invasions may alter this dynamic.

The Hawaiian archipelago is vulnerable to introductions of non-native species, due to its isolated location where ecosystems historically have been subjected to little change (Carlquist 1974; Vitousek et al. 1987; Cox et al. 2013). Since the 1950s, 20 different macroalgal species have been identified as introduced, of which six are recognized as invasive: *Acanthophora spicifera, Avrainvillea lacerata, Eucheuma denticulatum, Gracilaria salicornia, Hypnea musciformis* and *Kappaphycus alvarezii*, all present on the island of Oʻahu, where the majority of the introductions were initiated (Smith et al. 2002; Carlton and Eldredge 2009; Cox et al. 2013). Most focus has been on negative effects by algal introductions on reef building corals, but there are also indications that invasive algae monopolize habitat at the expense of native algal communities (Lapointe and Bedford 2011). Native macroalgae, or *limu*, play important roles in the Hawaiian culture, and are used as food, medicine and for spiritual purposes (Abbott 1978, 1992; Cox et al. 2013; McDermid et al. 2019). Ecologically, *limu* are important primary producers, contributing to carbon and nutrient flows and provide key ecological functions such as nursery and feeding habitat for fish and invertebrates (Fulton et al. 2019, 2020; McDermid et al. 2019).

This study aims to explore differences between native and non-native invasive macrophytes from a representative subset of the species pool in the Main Hawaiian Islands (MHI) by using a trait-based approach and discussing potential additions or losses of ecological traits in the invaded communities. We hypothesize that there will be differences in functional traits between the native and non-native algal group, and that this difference may be more pronounced for functional traits that relate to interactions among species, such as competitive abilities. To explore the feasibility of this approach in revealing mechanisms underlying how nuisance and potentially invasive algae may fit into a recipient ecosystem and estimate their potential to become invasive, the recently described alga *Chondria tumulosa* Sherwood and Huisman (2020), (Sherwood et al. 2020) is included as a case study. Although *C. tumulosa* is not yet confirmed from the MHI, evidence from the Papahānaumokuākea Marine National Monument (PMNM) in the northwestern Hawaiian archipelago suggests that it may have the potential to become invasive if introduced (Sherwood et al. 2020; Fumo et al. 2024). We therefore evaluate whether this species clusters in trait space with other invasive species. Two types of functional traits are investigated; first, traits that are related to ecological niche space/habitat selection (e.g., salinity tolerance and depth), second, traits that are related to interactions among reef plants and may affect competitive abilities/ecological success (e.g., growth rates and reproduction strategies). Finally, differences in functional traits between native and invasive non-native species and potential ecosystem effects of an invasion of *C. tumulosa* are discussed.

Methods

Study species and functional traits

In order to select commonly occurring macrophytes in Hawaiian waters, species were derived from five different comprehensive inventory studies; one from the PMNM (Vroom and Braun 2010) and four from the MHI (Carlton and Eldrige 2009; Cox et al 2013; LaValle et al. 2020; Fuller et al. 2024). This was complimented by a species list from the course "Quantitative Underwater Ecological Surveying Techniques" (QUEST), taught to research divers at the University of Hawaiʻi and tailored by phycologists over the last nearly 50 years to include the commonest species encountered in Hawaiʻi (Table 1). All species observed in the five field studies and listed in QUEST were included, and two species (*Centroceras clavulatum* and *Dictyopteris australis*) were added due to personal observations of the authors, although not listed in the described studies. Three species were excluded (*Caulerpella ambigua*, *Jania* sp, and *Wrangelia elegantissima*) because literature data (e.g. growth rate, salinity tolerance, depth preferences, palatability) were lacking for a majority of the chosen traits. This resulted in a total of 96 macrophytes; 39 belonging to rhodophyta, 22 belonging to phaeophyceae, 30 belonging to chlorophyta, one species of ochrophyta, three cyanobacteria and one seagrass species (Table 1). Of these, eight were non-native, 87 were putatively native to Hawaiʻi (Carlton and Eldredge

Table 1 The macrophyte species that were included in the study. "Origin and invasive potential" describes if a species is native to Hawai'i or not and "Reference occurrence" denotes which study the species in question was derived from

Phyla	Species	Origin and invasive potential	Reference origin	Reference occurrence
Rhodophyta	*Acanthophora pacifica*	Native	Kraft (1979), Huisman et al. (2007)	Cox et al. (2013), LaValle et al. (2020), Fuller et al. (2024); QUEST
	Acanthophora spicifera	Invasive non-native	Doty (1961), Kraft (1979), Smith et al. (2002)	Smith et al (2002), Carlton and Eldrige (2009)
	Amansia glomerata	Native	Agardh (1822), Rock (1913), Abbott (1999), Huisman et al. (2007)	QUEST
	Asparagopsis taxiformis	Native	Chamberlain (1880), Abbott (1984), Abbott (1999), Huisman et al. (2007)	Vroom and Braun (2010), Cox et al. (2013), QUEST
	Botryocladia skottsbergii	Native	Magruder and Hunt (1979), Huisman et al. (2007)	Cox et al. (2013)
	Centroceras clavulatum	Native	Chamberlain (1880), Setchell (1905), Abbott (1999), Huisman et al. (2007)	This study
	Chondria tumulosa	Invasive non-native	Sherwood et al. (2020)	Sherwood et al. (2020)
	Dasya iridescens	Native	Schlech (1990), Huisman et al. (2007)	Vroom and Braun (2010); Quest
	Dichotomaria marginata	Native	Butters (1911), Papenfuss et al. (1982)	Fuller et al. (2024); QUEST
	Dudresnaya hawaiiensis	Native	Lee (1963), Robins and Kraft (1985), Abbott (1999), Huisman et al. (2007)	This study
	Eucheuma denticulatum	Invasive non-native	Glenn and Doty (1981), Abbott (1999), Smith et al. (2002)	Smith et al. (2002), Carlton and Eldrige (2009)
	Galaxaura rugosa	Native	Magruder and Hunt (1979), Abbott (1999), Huisman et al. (2007)	Vroom and Braun (2010), Cox et al. (2013)
	Ganonema farinosum	Native	Abbott (1945, 1984)	Vroom and Braun (2010)
	Gibsmithia hawaiiensis	Native	Doty (1963), Magruder and Hunt (1979), Huisman et al. (2007)	QUEST
	Gracilaria cornopifolia	Native	Harvey and Bailey (1851), Agardh (1852), Huisman et al. (2007)	QUEST
	Gracilaria salicornia	Invasive non-native	Abbott (1999), Smith et al. (2002, 2004)	Smith et al. (2002), Carlton and Eldrege (2009), Cox et al. (2013), Fuller et al. (2024); QUEST
	Gracilaria tikvahiae	Invasive non-native	Abbott (1987), Abbott (1999), Carlton and Eldredge (2009)	Carlton and Eldredge (2009)
	Grateloupia filicina	Native	Chamberlain (1880), Setchell (1905), Huisman et al. (2007)	QUEST
	Gymnogongrus durvillei	Native	Agardh (1847), Abbott (1999), Huisman et al. (2007)	Fuller et al. (2024); QUEST

Table 1 (continued)

Phyla	Species	Origin and invasive potential	Reference origin	Reference occurrence
	Haloplegma duperreyi	Native	Doty et al. (1974)	Vroom and Braun (2010)
	Halymenia spp	Native	Chamberlain (), Rock (1913)	QUEST
	Hypnea cervicornis	Native	Mshigeni (1978), Abbott (1981)	Cox et al. (2013)
	Hypnea chordacea	Native	Mshigeni (1978), Magruder and Hunt (1979)	Cox et al. (2013)
	Hypnea musciformis	Invasive non-native	Abbott (1987), Smith et al. (2002), Vermeij et al. (2009)	Cox et al. (2013), Fuller et al. (2024); QUEST
	Kallymenia thompsonii	Native	Abbott and McDermid (2002	Vroom and Braun (2010)
	Kappaphycus alvarezii	Invasive non-native	Doty (1985), Abbott (1999), Smith et al. (2002)	Carlton and Eldredge (2009), Fuller et al. (2024)
	Laurencia dendroidea	Native	Tsuda (1965), Abbott (1999), Huisman et al. (2007)	This study; Vroom and Braun (2010)
	Laurencia mcdermidae	Native	McDermid (1988), Smith (1992)	Cox et al. (2013)
	Liagora spp (*Liagora divaricata/perennis*)	Native	Abbott (1999), Huisman et al. (2007)	Vroom and Braun (2010); QUEST
	Martensia hawaiiensis	Native	Sherwood et al. (2019)	QUEST
	Martensia tsudae	Native	Sherwood et al. (2019)	QUEST
	Peyssonnelia spp	Native	Dickie (1877), Lemmermann (1905), Magruder and Hunt (1979)	Vroom and Braun (2010
	Portieria hornemannii	Native	Chamberlain (1880, 1881), Tsuda (1965), Abbott (1999), Huisman et al. (2007)	Vroom and Braun (2010); QUEST
	Predaea weldii	Native	Kraft and Abbott (1971), Huisman et al. (2007)	QUEST
	Pterocladiella caerulescens	Native	Reed (1907), MacCaughey (1918), Abbott (1999), Huisman et al. (2007)	Cox et al. (2013); QUEST
	Pterocladiella capillacea	Native	Reed (1907), Abbott (1999), Huisman et al. (2007)	Cox et al. (2013); QUEST
	Ramicrusta hawaiiensis	Native	Sherwood et al. (2021)	Fuller et al. (2024)
	Tolypiocladia glomerulata	Native	Doty et al. (1974)	QUEST
	Trichogloea requienii	Native	Papenfuss (1946), Huisman et al. (2007)	Cox et al. (2013); QUEST
Phaeophyceae	*Asteronema breviarticulatum*	Native	Tsuda (1965), Ravanko (1970)	Cox et al. (2013)
	Chnoospora implexa	Native	Agardh (1848), Lemmermann (1905), Magruder and Hunt (1979)	Cox et al. (2013)

Table 1 (continued)

Phyla	Species	Origin and invasive potential	Reference origin	Reference occurrence
	Colpomenia sinuosa	Native	Chamberlain (1880), Abbott and Huisman (2004)	Cox et al. (2013); QUEST
	Dictyopteris australis	Native	Chamberlain (1880), Abbott and Huisman (2004), Huisman et al. (2007)	This study
	Dictyota acutiloba	Native	Agardh (1848), Rock (1913), Abbott and Huisman (2004), Huisman et al. (2007)	Cox et al. (2013), Fuller et al. (2024)
	Dictyota ceylanica	Native	Setchell (1905), Magruder and Hunt (1979), Abbott and Huisman (2004)	Vroom and Braun (2010)
	Dictyota friabilis	Native	Tilden (1901), Tsuda (1965), Agegian and Abbott (1985)	Vroom and Braun (2010)
	Dictyota sandvichensis	Native	Agardh (1848), Reed (1907), Magruder and Hunt (1979)	Vroom and Braun (2010), Cox et al. (2013)
	Distromium flabellatum	Native	Abbott and Huisman (2004)	Vroom and Braun (2010)
	Hydroclathrus clathrathus	Native	Chamberlain (1880), Tsuda (1965), Magruder and Hunt (1979)	Cox et al. (2013); QUEST
	Lobophora obscura	Native	Tilden (1901), Tsuda (1965), Agegian and Abbott (1985)	Vroom and Braun (2010), Cox et al. (2013), Fuller et al. (2024); QUEST
	Padina australis	Native	Magruder and Hunt (1979), Abbott and Huisman (2004), Huisman et al. (2007)	Fuller et al. (2024)
	Padina sanctae-crucis	Native	Magruder and Hunt (1979), Abbott and Huisman (2004), Huisman et al. (2007)	Huisman et al. (2007), Vroom and Braun (2010); QUEST
	Padina thivyae	Native	Doty and Newhouse (1966), Magruder and Hunt (1979), Huisman et al. (2007)	Huisman et al. (2007), Vroom and Braun (2010); QUEST
	Sargassum aquifolium	Native	Magruder (1988), Abbott and Huisman (2004), Huisman et al. (2007)	Fuller et al. (2024); QUEST
	Sargassum obtusifolium	Native	Gaudichaud (1826), Maguder (1988)	Fuller et al. (2024); QUEST
	Sargassum polyphyllum	Native	Gaudichaud (1826), Magruder (1988), Abbott and Huisman (2004), Huisman et al. (2007)	QUEST
	Sphacelaria novae-hollandiae	Native	Agegian and Abbott (1985), Huisman et al. (2007)	Huisman et al. (2007), Cox et al. (2013)
	Sphacelaria rigidula	Native	Tilden (1901), Tsuda (1965), Huisman et al. (2007)	Huisman et al. (2007), Cox et al. (2013)
	Sphacelaria tribuloides	Native	Tilden (1901), Tsuda (1965), Huisman et al. (2007)	Huisman et al. (2007), Cox et al. (2013)

Table 1 (continued)

Phyla	Species	Origin and invasive potential	Reference origin	Reference occurrence
	Stypopodium flabelliforme	Native	Doty and Newhouse (1966), Doty et al. (1974), Magruder and Hunt (1979), Huisman et al. (2007)	Vroom and Braun (2010); QUEST
	Turbinaria ornata	Native	Agardh (1848), Tilden (1901), Tsuda (1965), Abbott and Huisman (2004), Huisman et al. (2007)	Vroom and Braun (2010), LaValle et al. (2020), Fuller et al. (2024); QUEST
Chlorophyta	*Avrainvillea erecta*	Invasive non-native	Wade et al. (2018), Sherwood and Guiry (2023a, b)	QUEST
	Avrainvillea lacerata	Invasive non-native	Brostoff (1989), van de Verg and Smith (2022), Thornton et al. (2024)	Fuller et al. (2024)
	Boodlea composita	Weedy native	Chamberlain (1880, 1881), Setchell (1926), Huisman et al. (2007)	Vroom and Braun (2010)
	Bornetella sphaerica	Native	Egerod (1952), Tsuda (1965), Magruder and Hunt (1979), Abbott and Huisman (2004)	Cox et al. (2013)
	Bryopsis pennata	Native	Chamberlain (1880), Tsuda (1965), Abbott and Huisman (2004), Huisman et al. (2007)	Vroom and Braun (2010); QUEST
	Caulerpa racemosa	Native	Chamberlain (1880), Eubank (1946), Agegian and Abbott (1985), Abbott and Huisman (2004)	Vroom and Braun (2010); QUEST
	Caulerpa serrulata	Native	Howe (1934), Eubank (1946), Tsuda (1965), Abbott (1984)	Vroom and Braun (2010
	Caulerpa sertularioides	Native	Eubank (1946), Magruder and Hunt (1979), Abbott and Huisman (2004), Huisman et al. (2007)	Fuller et al. (2024); QUEST
	Caulerpa taxifolia	Native	Chamberlain (1880), Lemmermann (1905), Eubank (1946), Magruder and Hunt (1979), Abbott and Huisman (2004)	Vroom and Braun (2010), Fuller et al. (2024); QUEST
	Caulerpa webbiana	Native	Eubank (1946), Tsuda (1965), Abbott and Huisman (2004)	Vroom and Braun (2010)
	Chaetomorpha antennina	Native	Tilden (1901), Reed (1907), Tsuda (1965), Abbott and Huisman (2004	Fuller et al. (2024)
	Cladophora sericea	Native	Abbott and Huisman (2004), Smith et al. (2005)	QUEST
	Codium arabicum	Native	Tilden (1901), Reed (1907), Tsuda (1965), Abbott (1989)	Fuller et al. (2024)

Table 1 (continued)

Phyla	Species	Origin and invasive potential	Reference origin	Reference occurrence
	Codium edule	Native	Egerod (1952), Tsuda (1965), Abbott and Huisman (2004)	Cox et al. (2013), Vroom and Braun (2010); QUEST
	Codium reediae	Native	Chamberlain (1880), Egerod (1952), Abbott and Huisman (2004), Huisman et al. (2007)	QUEST
	Dictyosphaeria cavernosa	Weedy native	Chamberlain (1880), Tilden (1901), Egerod (1952), Tsuda (1965), Stimson et al. (2001), Abbott and Huisman (2004), Huisman et al. (2007)	Vroom and Braun (2010), Cox et al. (2013), Fuller et al. (2024); QUEST
	Dictyosphaeria verslusyii	Native	Setchell (1926), Howe (1934), Egerod (1952), Huisman et al. (2007)	Vroom and Braun (2010), Cox et al. (2013), Fuller et al. (2024); QUEST
	Halimeda discoidea	Native	Howe (1934), Egerod (1952), Abbott and Huisman (2004), Huisman et al. (2007)	Vroom and Braun (2010), Cox et al. (2013), Fuller et al. (2024); QUEST
	Halimeda distorta	Native	Tsuda (2014), Sherwood and Guiry (2023a, b)	Vroom and Braun (2010)
	Halimeda gracilis	Native	Gilbert (1962), Abbott and Huisman (2004)	Vroom and Braun (2010)
	Halimeda kanaloana	Native	Verbruggen et al. (2006), Huisman et al. (2007)	QUEST
	Halimeda opuntia	Native	Dickie (1877), Lemmermann (1905), Howe (1934), Magruder and Hunt (1979), Abbott and Huisman (2004)	Vroom and Braun (2010), Fuller et al. (2024); QUEST
	Halimeda velasquezii	Native	Abbott (1989), Abbott and Huisman (2004)	Vroom and Braun (2010)
	Microdictyon setchellianum	Native	Egerod (1952), Abbott (1989), Abbott and Huisman (2004), Huisman et al. (2007)	Vroom and Braun (2010), Cox et al. (2013); LaValle et al. (2020); QUEST
	Neomeris annulata	Native	Egerod (1952), Abbott and Huisman (2004), Huisman et al. (2007)	Vroom and Braun (2010), Cox et al. (2013); QUEST
	Ulva flexuosa	Native	Lemmermann (1905), Reed (1907), Tsuda (1965), Abbott and Huisman (2004)	Cox et al. (2013)
	Ulva lactuca	Weedy native	Gaudichaud (1826), Tilden (1901), Abbott and Huisman (2004), Huisman et al. (2007), Dailer et al. (2012)	Cox et al. (2013); QUEST
	Ulva prolifera	Native	Tilden (1901), Reed (1907), Abbott and Huisman (2004)	Fuller et al. (2024); QUEST
	Ulva reticulata	Native	Gilbert (1962), Doty et al. (1974), Magruder and Hunt (1979), Abbott and Huisman (2004)	Cox et al. (2013)

Table 1 (continued)

Phyla	Species	Origin and invasive potential	Reference origin	Reference occurrence
	Valonia ventricosa	Native	Egerod (1952), Agegian and Abbott (1985), Huisman et al. (2007)	QUEST
Ochrophyta	*Chrysocystis fragilis*	Native	Dollar and Grigg (2004)	Fuller et al. (2024)
Tracheophyta	*Halophila hawaiiana*	Native	Short (2003), Huisman et al. (2007)	QUEST
Cyanophyta	*Leptolyngbya crosbyana*	Native	Huisman et al. (2007)	Fuller et al. (2024)
	Lyngbya majuscula	Weedy native	Huisman et al. (2007), Arthur et al. (2008), Nelson et al. (2015)	QUEST
	Symploca hydnoides	Native	Huisman et al. (2007)	Fuller et al. (2024); QUEST

2009) and one, *C. tumulosa,* was cryptogenic (i.e., of unknown origin). We use the US Federal Government definition of an invasive species, which states that an invasive species is “a species not native to the region or area whose introduction (by humans) causes or is likely to cause harm to the economy or the environment, or harms animal or human health.” (National Invasive Species Council 2005). Although this definition does not categorize *C. tumulosa* as an invasive because of its unknown origin, we have chosen to include it in the invasive group, considering its highly invasive characteristics and its sudden appearance in the PMNM, among other traits as likely indications of non-native status (see Carlton and Schwindt 2024). Species of native status that displayed invasive characteristics were termed “weedy” instead of “invasive”. *Liagora divaricata* and *L. perennis* were pooled because these species are highly similar in habitat preferences, ecology and in physical appearance (Huisman et al. 2007), making field identifications uncertain.

Chondria tumulosa displays extreme weedy characteristics and is currently only known from the PMNM (Sherwood et al. 2020). This alga was first observed in 2016 at Manawai (Pearl and Hermes Atoll), exhibiting a thick, mat-like morphology, smothering and killing underlying flora and fauna (Sherwood et al. 2020; Lopes et al. 2023). The species is now established at Kuaihelani and Hōlanikū to the northwest of Manawai (Lopes et al. 2023). Despite the biogeographic barrier just to the southeast of Manawai (Toonen et al. 2011; Fumo and Sherwood 2023), it remains possible that this alga is capable of dispersal into the MHI (Fumo et al. 2024). The introduction of *C. tumulosa* in the MHI would likely have negative ecological effects on local flora and fauna, due to its weedy and invasive characteristics (Sherwood et al. 2020; Fumo et al. 2024).

The additional macrophytes were selected based on their common occurrence around Oʻahu and their presence across diverse habitats. This selection criterion draws from terrestrial plant ecology studies, which demonstrate that abundant species exert a disproportionately large influence on ecosystem functioning (Gaston 2010; Kaushik et al. 2022). Moreover, common species often play a key role in defining and shaping ecosystems, because their abundance makes them ecologically significant, as they contribute substantially to both ecosystem structure and functions (Smith and Knapp 2003; Gaston and Fuller 2008).

A total of 15 functional traits (both continuous and categorical) were selected, mainly based on the review by Nyberg and Wallentinus (2005) who applied functional traits to predict an invasive potential for an alga. Data for all traits included in the study were drawn from literature (Table 2, Online Resource 1). For species where no literature data was available for the specific traits, assumption-based data from related species were used (Online Resource 1). When information for a specific trait was missing without possibilities to extrapolate from other species, that trait category was excluded from the study. Functional traits were assigned to two different categories depending on type; (1) traits related to habitat selection/niche occupation, and (2) species interactions traits. Due to the strong environmental filtering effect wave exposure can impose on marine organisms, both producers and consumers (Dayton 1975; Bejarano et al. 2017), and its positive impact on primary production (Leigh et al 1987; Roff et al. 2015) and dispersal due to fragmentation of macrophytes, the trait "wave exposure score", i.e. the degree of wave exposure a species tolerate, was included in both categories (Table 2). Trait categorization was applied in order to reduce complexity of the statistical analysis and increase interpretation of the results, as analyzing all traits simultaneously may lead to masking of distinct patterns and thus less ecologically meaningful (Lavorel and Garnier 2002; Violle et al. 2007).

Category A, habitat selective traits, included six traits: "minimum salinity", "maximum salinity", "minimum depth", "maximum depth", "wave exposure" and "substrate", which all describe occupied habitat/niche. Category B, species interaction traits, included nine traits. "Reproductive score" is linked to a species' ability to disperse and increase its presence in a location. For this trait, data was binned in intervals depending on life history, modified from definitions in Nyberg and Wallentinus (2005). "Growth strategy" corresponds to the capitalization of substrate by a species, "maximum size" reflects the ability to assimilate light and is listed as an invasive trait because a large thallus can shade other, smaller species, allow a species to outgrow predation by herbivores (Briggs et al. 2018) and also translates to substrate capitalization (depending on vertical or horizontal growth). We are aware that this application of macrophyte size is a simplification because size also impacts nutrient uptake and carbon acquisition, (Hein et al. 1995), relationships that were beyond the scope of this study to include. "Palatability" and "allelopathy" are both linked to competitive success, because top-down control induced by herbivores can decrease biomass of macroalgae and allelopathy may give species a competitive release and thus advantage over other species. Information about binning of these two traits into five categories can be found in Online Resource 2. "Seasonality" may impact competition among macrophytes because species with dramatic seasonal growth patterns may be displaced by species present year-round when resources become available during senescence. "Growth rate" allows a rapidly growing species to outgrow its competitors and efficiently invade new habitats. "Morphology", which here refers to functional growth form, is a widely used approach in ecological studies of macroalgae, closely linked to competition for resources such as nutrient uptake and light assimilation (see e.g., Littler and Littler 1980; Balata et al. 2011).

Statistical analyses

Ordination of macrophytes according to functional traits

To evaluate potential differences in functional traits between native and non-native macrophytes and how *C. tumulosa* might fit into the picture, a principal coordinate analysis (PCoA) was conducted.

All 96 macrophyte species were included and grouped according to origin (native or non-native) (Table 1). *Chondria tumulosa* was grouped in the non-native category, due to its invasive characteristics (Sherwood et al. 2020), hereafter called the invasive group. Two separate analyses were conducted, one for each category of traits (A and B, Table 2). The first analysis included "minimum salinity" (continuous), "maximum salinity" (continuous), "minimum depth" (continuous), "maximum depth" (continuous), "substrate" (categorical) and "wave exposure score" (categorical) and the second "growth strategy (categorical)", "reproductive score" (ordinal factor), "palatability" (ordinal factor), "allelopathy" (ordinal factor), "growth rate" (continuous), "size" (continuous), "seasonality" (dichotomous factor) and "wave

Table 2 Functional traits included in the study and how they were classified in the statistical analyses. A: habitat selective trait, B: species' interaction traits. A more detailed description of how the definitions were categorized can be found in Online Resource 1

Functional trait	Type	Range	Definition	Ecological significance
Minimum salinity^{A}	Continuous	0.01–30 (psu)	The minimum salinity where the species is found	Distribution and habitat preferences
Maximum salinity^{A}	Continuous	33–45 (psu)	The maximum salinity where the species is found	Distribution and habitat preferences
Minimum depth^{A}	Continuous	0.01–10 (m)	The minimum recorded depth of the species	Distribution and habitat preferences
Maximum depth^{A}	Continuous	3–150 (m)	The maximum recorded depth of the species	Distribution and habitat preferences
Wave exposure score^{A,B}	Categorical	1–6	1: Low 2: Low-intermediate 3: Intermediate 4: Intermediate-high 5: High 6: Low to high wave exposure	Distribution and habitat preferences, dispersal and growth, herbivory escape, resource acquisition capabilities
Substrate^{A}	Categorical	1–4	1: Hard (limestone and basalt) 2: Soft (psammophytic substrates) 3: Hard + soft 4. Hard/soft + epiphytic	Distribution and habitat preferences
Reproductive score^{B}	Ordinal	1–11 1–10	1: Dioecious gametophyte. Fertile only short period 2: Dioecious gametophyte. Fertile long/many periods 3: Monoecious gametophyte. Not self-fertile and only for short period 4: Monoecious gametophyte. Not self-fertile, long/many periods 5: Monoecious gametophyte. Self-fertile 6: Large part of thallus fertile short period 7: Large part of thallus fertile long/many periods 8: Asexual spores, sexual reproduction may or may not occur 9: Low/intermediate fragmentation rates, sexual reproduction may or may not occur 10: High fragmentation rates, sexual reproduction may or may not occur	Dispersal and growth/competition with other benthic species

Table 2 (continued)

Functional trait	Type	Range	Definition	Ecological significance
Growth strategy^B	Categorical/.ordinal	1–4	1: Solitary 2: Patch-forming (≤ 1 m in diameter) 3: Meadow-forming (psammophytic species, ability to create stands > 1 m in diameter) 4: Canopy-forming (ability to create stands > 1 m in diameter) 5: Mat-forming (ability to create stands > 1 m in diameter)	Habitat occupation and competition with other benthic species, habitat formers for associated species
Size^B	Continuous	3–> 200 (cm)	Maximum size (horizontally or vertically)	Resource competition (substrate, sunlight, nutrients) and herbivory escape
Palatability^B	Ordinal	1–5	1: None 2: Low 3: Medium 4: Medium–high 5: High	Vulnerability to top-down control/functionality as foraging grounds for herbivores
Allelopathy^B	Ordinal	1–5	1: None 2: Low 3: Medium 4: Medium–high 5: High	Resource competition (e.g. for substrate with other benthic organisms) and herbivory escape
Seasonality^B	Categorical/ordinal	0,1	0: Non-seasonal 1: Seasonal	Competition for substrate, habitat formers
Growth rate^B	Continuous	1–16 (%)	Percent biomass per day	Resource competition (substrate, sunlight, nutrients) and herbivory escape
Morphology/functional form^B	Categorical	1–12	1: Coarsely branched 2: Siphonous 3: Thick leathery 4: Combined 5: Foliose 6: Gelatinous 7: Jointed calcareous 8: Hollow spherical 9: Filamentous 10: Prostrate 11: Crustose 12: Tubular	Resource competition (nutrient acquisition), growth, habitat formers for associated organisms, implications for herbivory and interactions with other benthic species

exposure score" (categorical). Continuous variables were log(x + 1) transformed in order to reduce the risk of distances becoming skewed due to differences in scales among variable types (Pavoine et al. 2009).

Multidimensional functional space was computed using a modified Gower distance-based matrix from package ade4 (Dray and Dufour 2007). This type of Gower distance is suitable for mixed variables, and can also handle missing data (Pavoine et al. 2009), which was feasible because certain species were lacking data for a few trait categories. The representation of each variable in the global distance was computed by using the kdist function in the ade4 package (Dray and Dufour 2007; Pavoine et al. 2009). The Gower distance-based matrix was transformed to Euclidian distances by Lingoes (1971) transformation (Pavoine et al. 2009) and visualized using principal coordinates analysis (PCoA) displaying the first two axis.

All statistical analyses were conducted in R version 4.1.2 (R Core Team 2024) and figures edited in Inkscape 1.2 (Inkscape Developers 2022).

Results

Ordination of macrophyte species according to functional traits

Four of the functional traits in the habitat selective category; "minimum salinity", "maximum salinity", "substrate" and "wave exposure score" had high correlations (> 0.5) with each other, and were subsequently considered to be adequately represented in the distance matrix. The first axis of the PCoA explained 21.8%, and the second 16.2% of the observed variation (Fig. 1a). Species were organized into clusters and invasive species were present in almost all clusters with the exception of *Gracilaria salicornia*, which was slightly separated from clusters (Fig. 1a). Invasive species reported to be found growing together in previous studies were ordinated close to each other, such as *Eucheuma denticulatum* and *Kappaphycus alvarezii, Acanthophora spicifera* and *Hypnea musciformis* and *Avrainvillea erecta* and *A. lacerata. Chondria tumulosa* was ordinated in the same cluster as *G. tikvahiae,* an invasive species which is present on the MHI but not yet established (Fig. 1a).

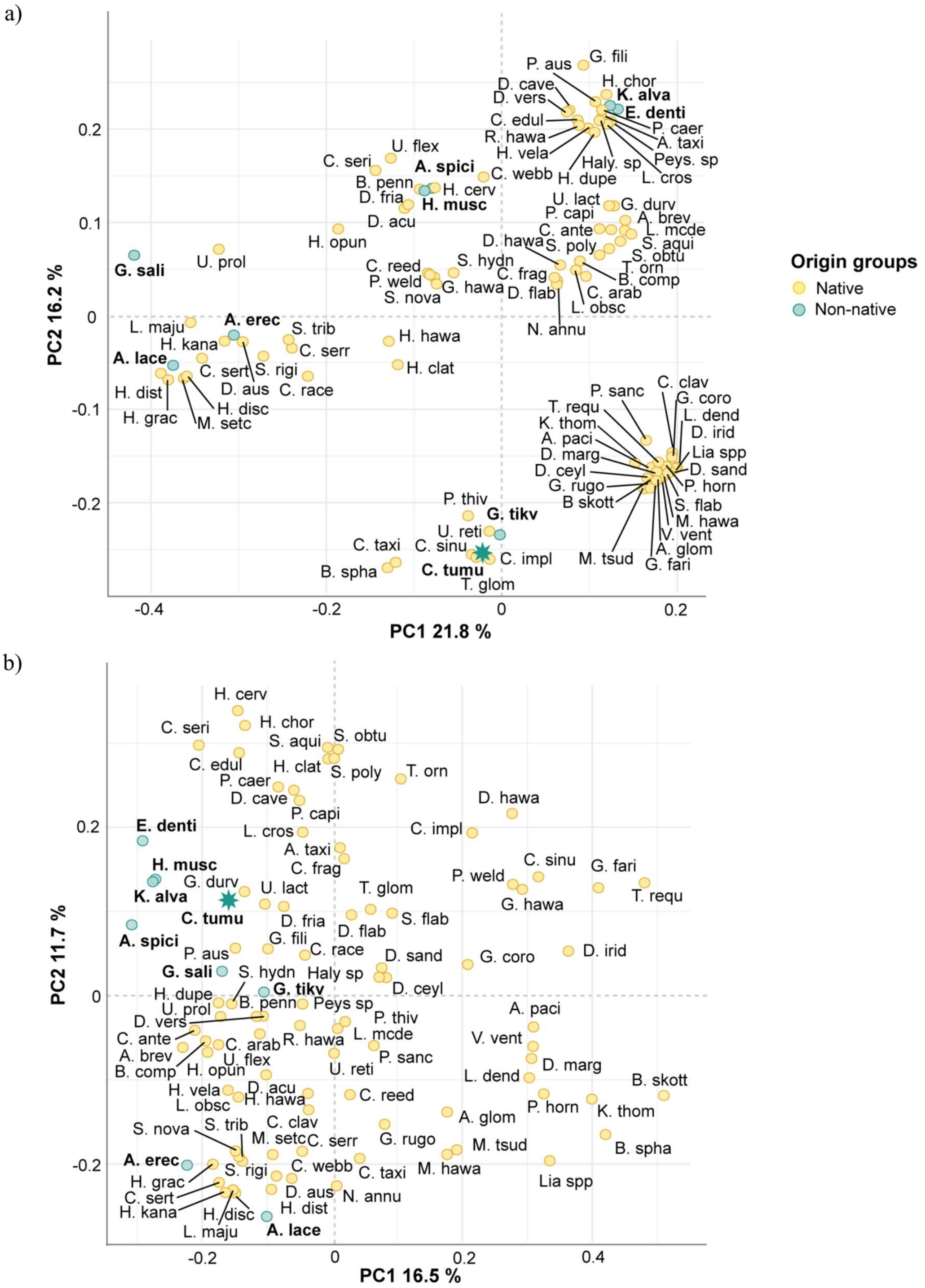
In the species interaction category, the functional trait "growth strategy" was the only one with a high (> 0.5) correlation value. Five traits had correlation values >0.3, which were "wave exposure score", "morphology", "palatability", "seasonality" and "reproductive score". The first axis of the PCoA explained 16.5%of the observed variation, and the second 11.7% (Fig. 1b). The invasive species clustered together with the exception for *A. erecta* and *A. lacerata,* which were organized together with the majority of the *Halimeda* species (Fig. 1b). In this category, *C. tumulosa* was clustered together with the majority of the invasive species, which were occupying a part of the distance matrix where few native species were found (Fig. 1b).

Discussion

Invasive macroalgae have introduced certain functional traits not previously found (or rarely found) in the shallow water habitats in the MHI, likely linked to their invasive success. Moreover, there was substantial overlap between the invasive and native macrophyte species for habitat selective traits, but less so for species' interaction traits. Habitats in the MHI which have shifted towards invasive algal communities where a few highly successful traits currently dominate, may experience a substantial decline in overall functional diversity. In the MHI, such areas are most common on the island of O'ahu, on the reefs outside Waikīkī and Kāne'ohe Bay bay (Smith et al. 2004; Neilson et al. 2018), and in the PMNM on Manawai (Sherwood et al. 2020; Lopes et al 2023). The results illustrate how this trait-based approach can be used to enhance our knowledge of ecological consequences of future and ongoing marine algal invasions.

There was a rather large overlap in habitat selective traits of native versus invasive macrophytes. The only alga that did not overlap with any other macrophyte was *G. salicornia,* probably because of this species' ability to thrive in hyposaline conditions and grow on both soft and hard substrates. However, this does not imply that *G. salicornia* complements the native species pool, because it is also found in high densities on reefs subjected to marine conditions where it aggressively outcompetes local flora and fauna (Smith et al. 2004). Rather, this illustrates that some species might not be one or the other (i.e. complementary or competitive), but instead capable of existing as both. This highlights the need to interpret results with caution combined with a solid ecological knowledge of the ecosystem in question. Considering the species interaction traits, overlaps between native and invasive algae were smaller and non-native invasives were organized close to each other, indicating similarities. Many of the invasive species shared traits such as a mat-forming growth strategy, a large thallus size, were non-seasonal and reproduced asexually by fragmentation. This aligns with our hypothesis, that differences in functional traits between the native and invasive groups are more pronounced for traits that are related to species interactions than for traits related to habitat selection.

The overlap in habitat selective traits between invasive and native algae illustrates that invasive


a)
PC1 21.8 %
PC2 16.2 %
-0.4
-0.2
0
0.2
-0.2
-0.1
0
0.1
0.2
P. aus
G. fili
H. chor
D. cave
K. alva
D. vers
E. denti
C. edul
P. caer
R. hawa
A. taxi
H. vela
Haly. sp
Peys. sp
H. dupe
L. cros
U. flex
C. seri
A. spici
C. webb
B. penn
H. cerv
D. fria
H. musc
D. acu
H. opun
U. lact
G. durv
P. capi
A. brev
C. ante
L. mcde
D. hawa
S. poly
S. aqui
S. obtu
T. orn
B. comp
C. arab
L. obsc
N. annu
C. frag
D. flab
C. reed
S. hydn
P. weld
G. hawa
S. nova
G. sali
U. prol
L. maju
A. erec
S. trib
H. kana
C. serr
A. lace
C. sert
S. rigi
C. race
D. aus
H. dist
H. disc
H. grac
M. setc
H. hawa
H. clat
P. sanc
C. clav
T. requ
G. coro
K. thom
L. dend
D. irid
A. paci
Lia spp
D. marg
D. sand
D. ceyl
P. horn
G. rugo
B skott
S. flab
M. hawa
V. vent
M. tsud
A. glom
G. fari
P. thiv
G. tikv
U. reti
C. taxi
C. sinu
C. impl
B. spha
C. tumu
T. glom
Origin groups
Native
Non-native
b)
PC1 16.5 %
PC2 11.7 %
-0.2
0
0.2
0.4
-0.2
0
0.2
H. cerv
H. chor
C. seri
S. obtu
S. aqui
C. edul
H. clat
S. poly
T. orn
P. caer
D. cave
D. hawa
P. capi
L. cros
C. impl
E. denti
A. taxi
C. frag
H. musc
C. sinu
G. fari
P. weld
G. durv
U. lact
T. glom
T. requ
K. alva
G. hawa
C. tumu
D. fria
S. flab
D. flab
A. spici
G. fili
C. race
D. sand
G. coro
D. irid
P. aus
G. sali
S. hydn
Haly sp
G. tikv
D. ceyl
H. dupe
B. penn
Peys sp
U. prol
A. paci
D. vers
P. thiv
L. mcde
C. ante
C. arab
R. hawa
V. vent
A. brev
U. flex
P. sanc
B. comp
H. opun
U. reti
D. marg
L. dend
B. skott
H. vela
D. acu
L. obsc
H. hawa
C. reed
P. horn
K. thom
S. nova
S. trib
C. clav
A. glom
M. setc
C. serr
G. rugo
M. tsud
B. spha
A. erec
S. rigi
C. webb
C. taxi
M. hawa
Lia spp
H. grac
C. sert
D. aus
N. annu
H. kana
H. disc
H. dist
L. maju
A. lace

◂**Fig. 1** Graphical representation of ordination of all species derived from the principal coordinate analysis (PCoA). The more similar species are, based on their functional traits, the closer they are organized together. Plots show **a** habitat selective traits, and **b** species interaction traits. The case study species, Chondria tumulosa, is indicated by a star, and invasive species are indicated by text in bold. *A. paci*= Acanthophora pacifica, *A. spici*= Acanthophora spicifera, *A. glom*= Amansia glomerata, *A. taxi*= Asparagopsis taxiformis, *A. brev*= Asteronema breviarticulatum, *A. erec*= Avrainvillea erecta, *A. lace*= Avrainvillea lacerata, *B. comp*= Boodlea composita, *B. spha*= Bornetella sphaerica, *B. skott*= Botryocladia skottsbergii, *B. penn*= Bryopsis pennata, *C. race*= Caulerpa racemosa, *C. serr*= Caulerpa serrulata, *C. sert*= Caulerpa sertularoides, *C. taxi*= Caulerpa taxifolia, *C. webb*= Caulerpa webbiana, *C. ante*= Chaetomorpha antennina, *C. clav*= Centroceras clavulatum, *C. impl*= Chnoospora implexa, *C. tumu*= Chondria tumulosa, *C. frag*= Chrysocystis fragilis, *C. seri*= Cladophora seriacea, *C. arab*= Codium arabicum, *C. edul*= Codium edule, *C. reed*= Codium reediae, *C. sinu*= Colpomenia sinuosa, *D. irid*= Dasya iridescens, *D. marg*= Dichotomaria marginata, *D. aus*= Dictyopteris australis, *D. cave*= Dictyosphaeria cavernosa, *D. vers*= Dictyosphaeria verslusyii, *D. acut*= Dictyota acutiloba, *D. ceyl*= Dictyota ceylanica, *D. frag*= Dictyota friabilis, *D. sand*= Dictyota sandvicensis, *D. flab*= Distromium flabellatum, *D. hawa*= Dudresnaya hawaiiensis, *E. denti*= Eucheuma denticulatum, *G. rugo*= Galaxaura rugosa, *G. fari*= Ganonema farinosum, *G. hawa*= Gibsmithia hawaiiensis, *G. coro*= Gracilaria coronopifolia, *G. sali*= Gracilaria salicornia, *G. tikv*= Gracilaria tikvahiae, *G. fili*= Grateloupia filicina, *G. durv*= Gymnogongrus durvillei, *H. disc*= Halimeda discoidea, *H. dist*= Halimeda distorta, *H. grac*= Halimeda gracilis, *H. kana*= Halimeda kanaloana, *H. opun*= Halimeda opuntia, *H. vela*= Halimeda velasquezii, *H. hawa*= Halophila hawaiiana, *H. dupe*= Haloplegma duperreyi, *Haly sp*= Halymenia *sp*, *H. clat*= Hydroclathrus clathratus, *H. cerv*= Hypnea cervicornis, *H. chor*= Hypnea chordacea, *H. musc*= Hypnea musciformis, *K. thom*= Kallymenia thompsonii, *K. alva*= Kappaphycus alvarezii, *L. dend*= Laurencia dendroidea, *L. mcde*= Laurencia mcdermidae, *L. cros*= Leptolyngbya crosbyana, *Lia spp*= Liagora dicaricata/perennis, *L. obsc*= Lobophora obscura, *L. maju*= Lyngbya majuscula, *M. hawa*= Martensia hawaiiensis, *M. tsud*= Martensia tsudae, *M. setc*= Microdictyon setchellianum, *N. annu*= Neomeris annulata, *P. aus*= Padina australis, *P. sanc*= Padina sanctae-crucis, *P. thiv*= Padina thivyae, *Peys sp*= Peyssonnelia *sp*, *P. horn*= Portieria hornemannii, *P. weld*= Predaea weldii, *P. caer*= Pterocladiella caerulescens, *P. capi*= Pterocladiella capillacea, *R. hawa*= Ramicrusta hawaiiensis, *S. aqui*= Sargassum aquifolium, *S. obtu*= Sargassum obtusifolium, *S. poly*= Sargassum polyphyllum, *S. nova*= Sphacelaria novae-hollandiae, *S. rigi*= Sphacelaria rigidula, *S. tribu*= Sphacelaria tribuloides, *S. flab*= Stypopodium flabelliforme, *S. hydn*= Symploca hydnoides, *T. glom*= Tolypiocladia glomerulata, *T. requ*= Trichogloea requienii, *T. orn*= Turbinaria ornata, *U. flex*= Ulva flexuosa, *U. lact*= Ulva lactuca, *U. prol*= Ulva prolifera, *U. reti*= Ulva reticulata, *V. vent*= Valonia ventricosa

species in the MHI can successfully establish themselves across a range of habitats, where they may outperform native species, as indicated by the different trait space occupied by the invasive algal group. This finding aligns with previous studies in plant ecology, where invasive species have flourished at the expense of native ones (MacDougall and Turkington 2005). In the MHI, invasive algae can be found from the shoreline to mesophotic depths (~ 0 to 90 m), on both hard and soft substrates, where they risk to become competitive superior (Veazey et al 2019). The results suggests that in areas where certain types of invasive algae are dominant, a substantial amount of functional diversity may be lost. Mat-forming invasive species, such as *Eucheuma denticulatum, G. salicornia* and *Kappaphycus alvarezii* all have the capacity to grow in high densities and efficiently outcompete other species (Kamalakannan et al. 2010; Martinez et al. 2012). Consequently, the habitats where these species dominate can become strikingly dissimilar in comparison to non-invaded areas (Martinez et al. 2012; Neilson et al. 2018), and thus drive local seascape modifications. Such modifications include transformations from high-complexity systems with canopy forming macroalgae and corals to less complex mat-forming algae, resulting in homogenization of the local seascape, loss of habitat structure and potentially reduced biodiversity (Strain et al. 2014). Thick algal mats create unfavorable microhabitats due to alterations of physical and chemical conditions beneath them, such as low oxygen conditions, low irradiance and low pH values (Hauri et al. 2010; Martinez et al. 2012). Critical ecosystem functions provided by corals and macroalgae in coral reef ecosystems include calcium carbonate production and erosion, primary production in support of herbivory, secondary production and predation, and nutrient acquisition and release (Brandl et al. 2019). Establishment of a mat-forming invasive species may compromise a majority of these functions, in particular if the invader is not consumed by herbivores, as appears to be the case with *C. tumulosa*.

A mat-forming growth strategy, especially in combination with a large thallus size and rapid growth rates, are traits that are described from invasive species elsewhere (Nyberg and Wallentinus 2005). Introduced species with these traits should thus be a cause of concern because they have the potential to monopolize substrate, overgrow slower-growing species and outcompete species with a seasonal growth cycle, such as *Sargassum* spp., that once was common in nearshore areas on O‘ahu (Glenn et al. 1990; Smith et al. 2002; Kinzie 2008), and small gelatinous red algae with short seasonal appearances (Guimaraes and Amado-Filho 2008; Gabriel et al. 2017).

Large, canopy-forming algae (e.g., fucoids and *Sargassum* spp.) harbor high densities of epifauna (Råberg and Kautsky 2008; Hansen et al. 2010; Fraser et al. 2020; Chen et al. 2021) and often provide nursery and foraging habitats for fish (Fulton et al. 2020). Numerous studies have underscored the negative effects on biodiversity and ecological functions induced by regime shifts from coral to algal domination (Hughes et al. 1994; Bellwood et al. 2006; Pratchett et al. 2011, 2014), and highlighted that invasive species can amplify the occurrence, intensity and persistence of such shifts (Williams and Smith 2007; Fong and Paul 2011). Introduction of the nuisance species *Chondria tumulosa* to the MHI, would, as indicated by this study, likely not be an exception. Based on species interaction traits, this species was similar to the non-native macrophyte group (and also to the weedy native *Ulva lactuca*). One major difference however, is that both *E. denticulatum* and *K. alvarezii* in the invasive group are highly palatable and their biomass can be controlled by herbivores (Neilson et al. 2018; Eggertsen et al. 2021), which is not the case for *C. tumulosa,* which is thus far reported to be avoided by herbivores (Sherwood et al. 2020). Top-down control, which has shown to be a successful management strategy to control blooms of *E. denticulatum* and *K. alvarezii,* might thus not be a useful mitigation measure for *C. tumulosa*.

To what extent *C. tumulosa* can compete with the present flora and fauna on O‘ahu can only be speculated upon, yet the dominance of the species at Manawai implies the consequences may be dire. As opposed to the other invasive algae presented here, which largely occur between 1 and 3 m (with the exception of *Avrainvillea erecta* and *A. lacerata*), *C. tumulosa* can be found much deeper; it extends to 20 m with high biomass at 10–15 m (Sherwood et al. 2020). This alga may therefore pose a threat to the native algal species in the MHI (and corals/benthos), which until now have escaped competition with invasive algae due to their greater depth range. Several of these species may be susceptible to competition due to seasonal growth cycles, small sizes and solitary or patchy growth forms. In addition, if established in high densities, an invader such as *C. tumulosa* may also reduce ecological functionality of the local coral reefs, which further can result in habitat loss, impairment of nutrient transfers from primary producers to higher trophic levels and disturbances to nutrient acquisition and retention within the ecosystem (Brandl et al. 2019).

The invasive algae in the MHI have a set of traits that have enabled them to be successful on O‘ahu, and it is highly likely that *C. tumulosa* may be equally successful, but with the additional possibility to extend to and dominate in deeper reef areas. Another reason for concern is the dispersal potential of *C. tumulosa* which is linked to its substrate preferences. Similar to *A. spicifera* and *H. musciformis, C. tumulosa* has the ability to disperse via drifting fragments or rafting i.e., hitchhiking by attaching itself to other species or floating objects (Smith et al. 2002; Vermeij et al. 2009; Fumo et al. 2024). An introduction of *C. tumulosa* to the MHI would likely result in rapid dispersal with distribution patterns potentially equal to that of *A. spicifera* (Smith et al. 2002; O’Doherty and Sherwood 2007). This dispersal potential is in contrast to the other invasive mat-forming species such as *E. denticulatum, G. salicornia* and *K. alvarezii,* which all have restricted distributions in the MHI due to their dispersal strategies with negatively buoyant fragments that cannot be transported over long distances (Russell 1983; Smith et al. 2002).

In the MHI, shifts from functionally diverse native algal communities to assemblages dominated by invasive species may exhibit reduced functional diversity. Future studies of epifaunal assemblages of the different algal communities (native and non-native) and their roles as a key habitat for different life stages of fish are necessary to understand potential links between habitat shifts and higher trophic levels and subsequent ecosystem effects. Also, functional diversity models are only representatives of the traits that are chosen for the analyses. Several functional traits and more refined data sets for species, which may have improved the accuracy of the models, were excluded from this study due to a lack of published ecological information for many of the species in the study. These traits included temperature tolerance, nutrient-scape preferences and surface-to-volume ratios. Knowledge gaps as such should be addressed in future studies in order to refine and expand the applicability of trait-based models. Also, our study only contains a subset of the approximately 660 algal species present in Hawaiian waters (Sherwood and Guiry 2023a, b), and although it was not feasible to include all species in this review, the selection of species could have impacted the results.

In summary, our study indicates that *C. tumulosa* possesses a combination of traits that maximizes its potential for invasion and functional success in Hawai'i. We find it highly likely, that if introduced to the MHI, this species would be yet another driver in a shift towards low-complexity and low-diversity habitats. Eradications of introduced species are rarely successful and often costly, and might not be possible for *C. tumulosa* based on its functional traits. For this species, it is therefore critical to minimize the risk of it reaching the MHI.

Conclusions

We have demonstrated how trait-based analyses can provide a novel tool for evaluating the invasive potential of algal species using the Hawaiian flora as a case study. Applying these analyses to the algal community of the Hawaiian archipelago clearly showed that there are pronounced differences in functional traits between native and non-native algal communities accompanied by a substantial decline in overall functional richness in areas dominated by non-native algae. The introductions of invasive macroalgae have led to habitats characterized by species with a few highly successful traits that were uncommon before their arrival, and which decrease the habitat suitability for many other species. The results from this study also indicate that the newly described *Chondria tumulosa* has high potential of establishing and becoming invasive in the MHI. In short, *C. tumulosa* shared functional traits that are shown to be highly competitive in successful invasive algal species in Hawai'i, such as a mat-forming tendency, a large size, reproduction through fragmentation and the ability to grow both on soft and hard substrate and as an epiphyte. An alga that possesses these traits should be considered as having a high invasive potential.

Acknowledgements The authors are grateful to the Associate Editor and the two anonymous reviewers for considering this work and providing valuable feedback which improved the quality of the manuscript substantially.

Author contributions All authors contributed to the writing and development of the manuscript. Data collection was conducted ME and JTF with advice from CMS. Conceptualization and analysis were conducted by ME with valuable input from JTF, ARS, UB and LMR. The first draft of the manuscript was written by ME and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Funding Open access funding provided by Swedish University of Agricultural Sciences. ME was funded by The Swedish Research Council [2022-00338] and received additional support from the Sweden-America Foundation. LMR was funded by FORMAS through an early -career researcher grant [2021-00550].

Data availability statement All data supporting the findings of this study are available within the paper and its supplementary information (Online Resource 1).

Declarations

Competing interests The authors have no relevant financial or non-financial interests to disclose.

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