



Epibiont communities on stranded kelp rafts of *Durvillaea antarctica* (Fucales, Phaeophyceae)—Do positive interactions facilitate range extensions?

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Abstract

Aim: This study examines how rafting on floating bull kelps can shape the biogeographic patterns of raft-associated species, and analyses the spatio-temporal variability of taxonomic richness and co-occurrences of epibionts on beach-cast rafts of *Durvillaea antarctica* along a latitudinal gradient.

Location: Southeast Pacific, along ~1,700 km of coastline.

Methods: We examined the epibionts on stranded individuals of *D. antarctica* on 33 beaches along the continental coast of Chile (28° S–42° S) within four biogeographic districts during the winter and summer of two years (2014/2015–2015/2016). Taxonomic richness and co-occurrences of epibionts within a holdfast were examined. Known geographic ranges and rafting ranges were compared to determine possible range expansions via rafting dispersal.

Results: Sessile species were the most frequent epibionts. Taxonomic richness varied among biogeographic zones and seasons, and was higher between 33° S and 42° S than between 28° S and 33° S, particularly in summer compared to winter. Taxonomic richness decreased with floating time (indicated by the presence and size of *Lepas* spp.). Habitat-forming epibionts such as mytilid mussels, the polychaete *Phragmatopoma moerchi* and the seaweeds *Gelidium linguatum* and *Lessonia spicata* favoured co-occurrences of other species within a holdfast, suggesting a habitat cascade (i.e. biogenic holdfast—sessile eco-engineers—other epibionts), while the boring isopod *Limnoria chilensis* and the excavating limpet *Scurria scurra* were negatively correlated with many other species. Some rafting epibiont species with low dispersal ability were found more than 100–300 km outside of their known geographic ranges, with more extensive ephemeral range extensions at the southern edge of their respective ranges, probably facilitated by higher availability of rafts in those areas.

Main Conclusions: These findings confirm that raft-associated species are frequently dispersed outside their known geographic ranges, although these range extensions vary strongly depending on the availability and persistence of rafts, and on the biotic interactions within the rafting assemblage.

**KEYWORDS**

floating seaweeds, geographic range, habitat cascade, marine biogeography, rafting dispersal, range extension

1 | INTRODUCTION

Many molecular studies of epibiont species on floating seaweeds have indicated population connectivity through long-distance rafting (e.g. Nikula, Fraser, Spencer, & Waters, 2010; Nikula, Spencer, & Waters, 2013). However, there is little empirical information about the rafting process itself and about the organisms capable of enduring extensive voyages, even though this information is necessary to evaluate the importance of this dispersal mechanism in shaping the geographic ranges of rafting species.

Seaweeds are usually attached to rocks with a holdfast structure. Some seaweeds have large holdfasts that can serve as habitat for small species (e.g. Thiel & Vásquez, 2000). Strong storms or herbivores can cause seaweeds to detach from the rock and some species with high buoyancy, mainly brown algae, can remain afloat for a long time, supporting a diverse associate community (Thiel & Gutow, 2005). After detachment of floating seaweeds from the primary substratum, the number of associated organisms can drastically decrease, particularly that of mobile ones (e.g. Gutow, Giménez, Boos, & Saborowski, 2009; Miranda & Thiel, 2008), and subsequently epibiont communities tend to get homogenised while afloat (Gutow, Beermann, Buschbaum, Rivadeneira, & Thiel, 2015) because only organisms capable of competing and exploiting resources on the raft (mainly space and food) are capable to persist during long journeys (Thiel & Gutow, 2005). For example, Stoner and Greening (1984) reported low variability in the epibiont community cohabiting on pelagic *Sargassum*, according to raft age. Interactions among epibionts during rafting journeys are thus thought to determine the species that survive long trips and can reach new habitats (Thiel & Gutow, 2005). The size of seaweed rafts also has a strong influence on the density and species richness of the epibiont community, because large rafts can support more travellers (Thiel & Gutow, 2005; Vandendriessche, Vincx, & Degraer, 2007). While some studies have examined rafting assemblages at sea, in order to assess the contribution of rafting dispersal to population connectivity and structuring of geographic ranges, it is necessary to identify the species that return to the coast, which was done herein by using beach-cast rafts as a proxy for successful rafting events on adjacent rocky shores.

The extent of geographic ranges of marine benthic species is delimited by their physiological tolerances, biological interactions and their potential dispersal capabilities (e.g. Lester, Ruttenberg, Gaines, & Kinlan, 2007), either due to intrinsic (e.g. the presence of planktonic larvae or adult mobility) and extrinsic factors (e.g. availability of floating substrata, currents and local winds). Therefore, the dispersal ability of a species should be related to its geographic range. Nevertheless, epibiont species with low autonomous dispersal potential

(i.e. with direct development or low mobility) but found frequently on floating seaweeds often have wider ranges than can be explained by their intrinsic dispersal capabilities. In line with these observations, the current geographic ranges of rafting epibionts are hypothesised to depend on (a) the dispersal ability of the floating substratum and its availability in coastal areas, (b) the biological interactions among epibionts and (c) their biological traits favouring long-distance rafting journeys (Macaya, López, Tala, Tellier, & Thiel, 2016; Thiel & Gutow, 2005).

Herein we used the southern bull kelp *Durvillaea antarctica* (Chamisso) Hariot 1892 as a model-organism to examine the possible effect of rafting dispersal on the geographic ranges of epibiont species along a latitudinal gradient. *Durvillaea antarctica* has a wide distribution in the Southern Hemisphere, mainly in sub-Antarctic waters (Fraser, Thiel, Spencer, & Waters, 2010). In Chile, it is present from 30° S to Cape Horn (56° S), inhabiting rocky areas, exposed or semiexposed to waves, in the lower intertidal and shallow subtidal zone (Hoffmann & Santelices, 1997). It is a species with positive buoyancy that has 1–2 m of average length, and can reach up to 10 m and more than 20 kg of wet biomass (Hoffmann & Santelices, 1997), with high rafting potential at high latitudes (Tala, Penna-Díaz, Luna-Jorquera, Rothäusler, & Thiel, 2017). Many different associate species inhabit the coalesced holdfasts of benthic individuals (Santelices, Castilla, Cancino, & Schmiede, 1980).

Rafts of *D. antarctica* frequently wash up on sandy beaches within its geographic range (Duarte, Jaramillo, Contreras, Acuña, & Navarro, 2009), and stranded biomass tends to vary strongly among biogeographic districts (López, Macaya, Tala, Tellier, & Thiel, 2017), being highest in the northern-central (30° S–33° S) and southernmost districts (37° S–42° S). Stranded specimens are also frequently found outside their northern geographic limit (<30° S), showing indications of prolonged floating times (López et al., 2017). This suggests that the connectivity of *D. antarctica* populations (Fraser et al., 2010) and eventually also of associated epibionts is higher in some areas than in others, particularly in zones with high availability of rafts and less stressful conditions at the sea surface.

Herein we tested the following hypotheses: (a) species richness of epibionts on *D. antarctica* rafts increases along a latitudinal gradient because rafting dispersal opportunities increase in areas where environmental conditions at the sea surface are less severe (e.g. at high latitudes), (b) species richness of epibionts decreases with increasing floating time of stranded rafts, (c) range extensions of epibiont species are more common in the southern parts of the study area, where supplies of floating seaweeds are higher, (d) epibiont species are more frequently observed outside their geographic ranges on rafts with long floating times than on rafts with no



indication of floating or less floating time and (e) epibionts are more frequently observed outside of their geographic ranges on rafts with species that favour co-occurrences. In order to test these hypotheses, we determined the spatio-temporal variability of species richness and co-occurrences of epibionts on holdfasts of recently stranded *D. antarctica*, according to biogeographic districts of the Chilean coast (28° S–42° S) and floating times of stranded specimens. This information is used to evaluate the role of rafting dispersal by floating seaweeds as a modulator of the geographic ranges of benthic species commonly found on rafts.

2 | MATERIALS AND METHODS

2.1 | Characteristics of the study area

The continental coast of Chile (from approximately 28° S to 42° S) is characterized by a linear topography with a north–south orientation and the absence of distinct geographic barriers to dispersal of marine organisms (Camus, 2001). This area has a strong latitudinal gradient of sea surface temperature within the Humboldt Current System (Camus, 2001).

This study was conducted on 33 sandy and pebble/cobble beaches (28° S–42° S) across the benthic and pelagic geographic range of *D. antarctica* (Figure 1). Distances between adjacent beaches varied from 30 to 100 km and the extension of the stretches that were surveyed on each beach ranged from 0.28 to 11.08 km, depending on beach length and/or amounts of stranded bull kelps (for details see López et al., 2017). Beaches were distributed across the four biogeographic districts, based on Camus (2001) and a previous study (López et al., 2017): the southern edge of the Peruvian Province, 28° S–30° S, hereafter termed Coquimbo-Choros District (CCD); Septentrional District (SED), 30° S–33° S; Mediterranean District (MED), 33° S–37° S; Meridional District (MD), 37° S–42° S (Figure 1, see also Supporting Information Tables S1.1 and S1.2). A recent study showed that the stranding dynamics of *D. antarctica* vary strongly between these biogeographic districts (López et al., 2017); added to the genetic structure shown for this area by Fraser et al. (2010) (i.e. high genetic differentiation between nearby populations, 100–200 km), this suggests that rafting-mediated connectivity of populations of *D. antarctica* and its epibionts might also differ between these districts.

2.2 | Sampling and morphological measurements of stranded *Durvillaea antarctica*

Recently stranded individuals of *D. antarctica* were collected on each beach during winters and summers in two consecutive years (2014/2015 and 2015/2016). For the purpose of this study, only intact individuals with both fronds and holdfasts were considered. Likewise, because *D. antarctica* may present holdfasts with multiple stipes (each stipe corresponds to a different individual, González, Beltrán, Flores, & Santelices, 2015), for practical purposes hereafter a stranded specimen will be called a “plant”.

A total of 5,219 complete plants were measured during the study. For each complete plant of *D. antarctica*, the following variables were measured:

(BH) Biomass of holdfast: the wet weight of the holdfast was measured with a portable electronic hanging digital scale of 1 g accuracy.

(FT) Floating time: for each plant, we determined whether it had been colonised by stalked barnacles of the genus *Lepas* or not. The presence and size (i.e. capitular length) of these organisms can indirectly indicate the floating time of a substratum (Thiel & Gutow, 2005). Cyprid larvae and adult specimens of *Lepas* spp. were visible to the naked eye and verified from fronds and holdfasts of stranded bull kelps. According to the presence and size of stalked barnacles, all *D. antarctica* rafts were categorised in three groups: (a) short floating time (<2 days)—plants without any *Lepas*; (b) intermediate floating time (2–10 days)—plants with cyprid recruits or small, juvenile *Lepas* (<5 mm capitular length); and (c) long floating time (>10 days)—plants with large, adult *Lepas* (≥5 mm capitular length). For some specific analyses (see below in *Comparison of geographic ranges*), and due to the observed low frequency of rafts with large *Lepas* spp., the intermediate and long floating time categories were grouped, and only two categories were considered (absence and presence of *Lepas* spp.) (for details see Supporting Information Appendix S2).

2.3 | Taxonomic richness of epibionts

The presence of epibiont species on holdfasts was registered for each stranded bull kelp, checking both sides of each holdfast. Some species that were difficult to determine in the field were taken back to the lab for detailed species identification. Because we recorded many taxa at different levels of resolution (i.e. species, genus, order), we herein used the term “taxonomic richness” to represent putative species richness. For each *D. antarctica* plant, the number of epibiont species was calculated and considered as the taxonomic richness at the plant level. Mean values and standard deviations of taxonomic richness for total epibionts, only sessile and only mobile epibionts were calculated according to biogeographic district, year, season and floating time category, using the PRIMER v7 software (Clarke, Gorley, Somerfield, & Warwick, 2014).

Because the observed taxonomic richness of epibionts may be influenced by sampling effort and abundance of stranded bull kelps found on each beach, taxonomic richness was also estimated per beach using the Chao 2 index (hereafter named “accumulated taxonomic richness”) (Chao & Lee, 1992), calculating an average value and estimated standard deviation in the case of biogeographic district, year, season and floating time category, using the ‘vegan’ package (Oksanen et al., 2017) in R 3.4, (R Development Core Team, 2017). Details of the statistical analyses can be found in Supporting Information Appendix S2.

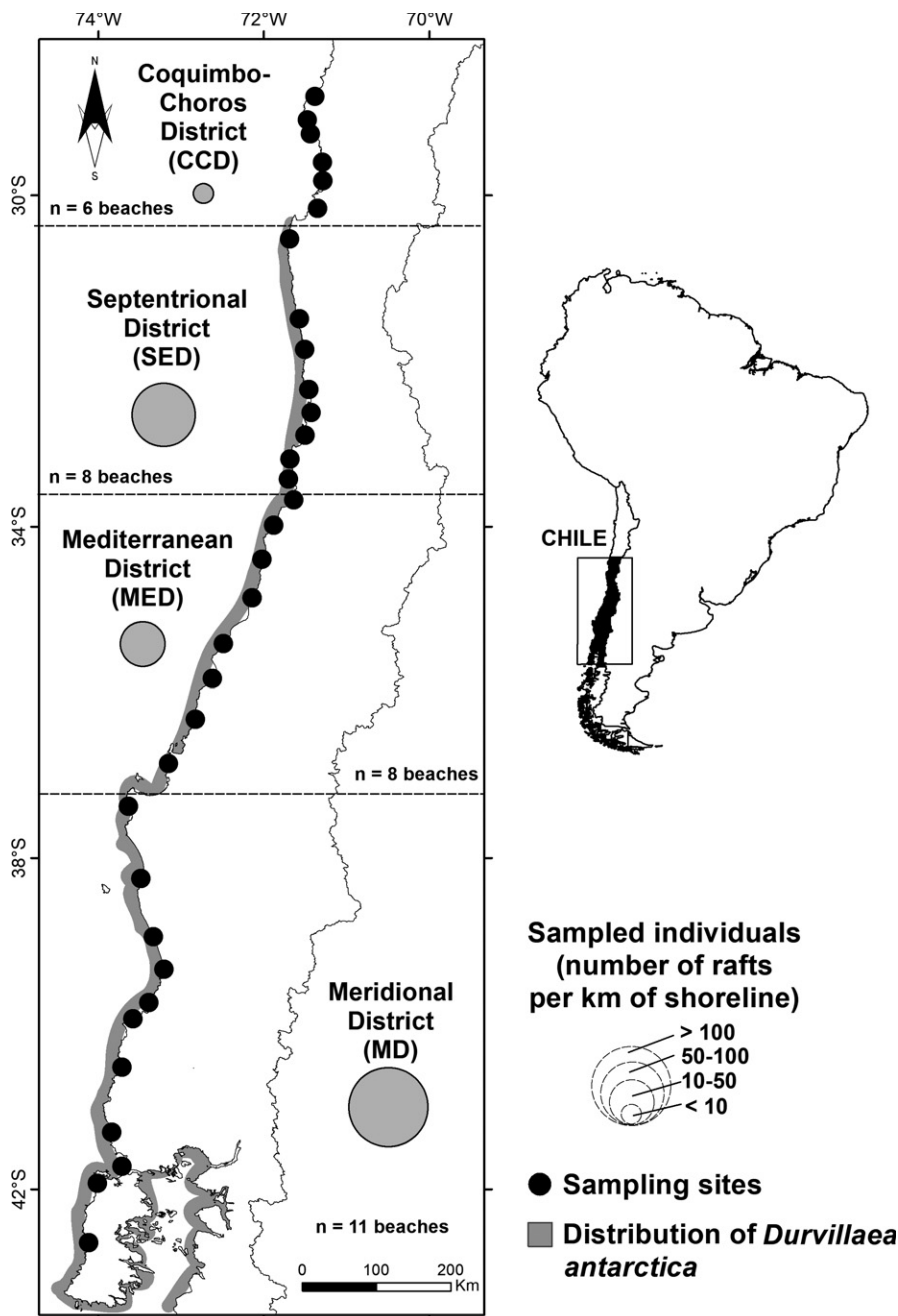


FIGURE 1 Geographic distribution of sampling sites and biogeographic districts described for the coast of Chile described in this study (Coquimbo-Choros District: 28° S–30° S, Septentrional District: 30° S–33° S, Mediterranean District: 33° S–37° S, Meridional District: 37° S–42° S). The geographic distribution of *Durvillaea antarctica* within the study area is also indicated. The number of beaches sampled within each biogeographic district is shown. The size of grey circles represents the sampled individuals of *D. antarctica* in each biogeographic district

2.4 | Co-occurrence of epibiont species

To analyse the co-occurrence of species within a single holdfast of stranded individuals of *D. antarctica*, we worked with a subset of 28 species (see Supporting Information Tables S4.1 and S4.2) that presented a minimum of 20 records within all plants sampled throughout the study. With these, the presence/absence matrices of epibiont species were constructed. Of a total of 300 pair combinations considered, 77 pairs (25.6%) were removed from the analysis because expected co-occurrence was <1, and thus only 223 pairs were analysed. The species co-occurrence matrix was calculated, showing positive co-occurrences (i.e. species tending to occur together), negative co-occurrences (i.e. species interfering with the

presence of others) and random co-occurrences (i.e. unrelated species) (Veech, 2014), using the package 'cooccur' (Griffith, Veech, & Marsh, 2016) in R 3.4 (R Development Core Team, 2017).

2.5 | Comparison of geographic ranges

From all epibiont species recorded on stranded bull kelps, 35 species were chosen for the range analysis that satisfied the following criteria: (a) identification to species level, (b) more than four records among the total of all stranded bull kelp rafts and (c) clear latitudinal delimitation of geographic range described in the specialized literature (Supporting Information Tables S3.1, S4.1 and S4.2). For these 35 species, a literature review was conducted to determine their



currently known geographic ranges along the Chilean coast, using specialized references for seaweeds and invertebrates (see more details in Supporting Information Table S3.1).

For each species, two types of ranges were considered: (a) the distribution range based on literature (hereafter called "literature range") and (b) the range determined by the presence on beach-cast bull kelps along the surveyed beaches (hereafter called "rafting range"); both ranges (literature and rafting) were expressed as latitudinal bins of 1°.

For the comparison of geographic ranges, species were grouped in three range categories: (a) species that presented rafting ranges within their reported literature ranges (hereafter called "range overlap", RO), (b) species that presented rafting ranges which extended beyond the southern edge of their known literature ranges (hereafter called "southward extension", SE) and (c) species that presented rafting ranges which extended beyond the northern edge of their literature ranges (hereafter called "northward extension", NE) (see more details, solid and dotted lines, below on map figure in Results). For each category, the number of raft-associated species was quantified according to both types of ranges (literature, rafting) per latitudinal bin of 1°. Thus, to determine whether the floating time of stranded *D. antarctica* (i.e. absence and presence of *Lepas* spp.) was associated with the probability of finding rafting epibionts outside their literature ranges, generalized linear models (GLM) were performed for SE and NE species separately (see details of statistical analyses in Supporting Information Appendix S2).

In order to examine if positive and negative co-occurrences correlate with the observed range expansions, we determined whether the presence or absence of two species with high positive co-occurrences (*Gelidium lingulatum* and *Semimytilus algosus*, see "Results") and of two species with high negative co-occurrences (*Limnoria chilensis* and *Scurria scurra*, see "Results") were correlated with the frequencies of stranded individuals of *D. antarctica* with epibionts found outside of their literature ranges, expressed as percentage per beach (i.e. SE and NE species, separately) (see details of statistical analyses in Supporting Information Appendix S2).

3 | RESULTS

A total of 89 epibiont taxa were recorded on holdfasts of stranded *D. antarctica*. Of the species found, 86.5% were sessile and 13.5% were mobile epibionts. Also, 71.9% were seaweeds and 28.1% were invertebrates. Within the seaweed group, 48 were Rhodophyta, 10 Phaeophyceae and 6 Chlorophyta, and several unidentified crustose calcareous algae (Supporting Information Table S4.1). With respect to invertebrates, the most common taxonomic groups were Cnidaria, Bryozoa, Mollusca, Annelida and Crustacea (Supporting Information Table S4.2, for more details see Supporting Information Appendix S4).

3.1 | Taxonomic richness

Taxonomic richness of epibionts ranged from 0 to 8 species per plant of *D. antarctica*, with an average of 2.6 ± 1.4 species. The

taxonomic richness of all epibionts observed per plant of *D. antarctica* differed significantly between seasons, and was higher in summer compared to winter ($p < 0.05$), but no differences were observed for other factors or interactions (Figure 2a and Supporting Information Figure S4.1a, Table S4.3). A significant relationship between taxonomic richness of epibionts and the holdfast wet weight of stranded individuals was observed (Supporting Information Figure S4.2). Accumulated taxonomic richness (Chao 2 index) varied significantly among biogeographic districts, years and seasons ($p < 0.05$), with higher taxonomic richness in high-latitude districts (CCD < SED < MED < MD) (Figure 2a), as well as in summer compared to winter (mainly in 2015) (Supporting Information Figure S4.1a).

Average taxonomic richness of sessile epibionts varied only among biogeographic districts and seasons (Figure 2b and

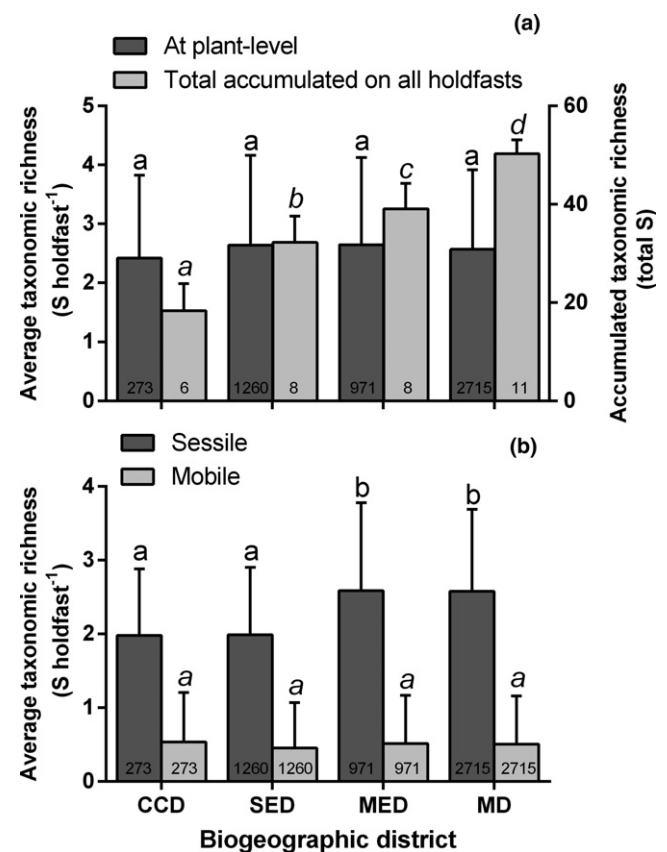


FIGURE 2 Average (mean \pm SD) taxonomic richness of epibionts attached on stranded individuals of *Durvillaea antarctica* on beaches from the continental coast of Chile (28° S–42° S), according to marine biogeographic districts (CCD: Coquimbo-Choros District; SED: Septentrional District; MED: Mediterranean District; MD: Meridional District). (a) Taxonomic richness at plant level and accumulated per beach in the different districts (Chao 2 index). (b) Average taxonomic richness of sessile and mobile epibionts. Letters (a-b-c-d) above the columns indicate significant differences between biogeographic districts ($p < 0.05$). Letters in italics correspond to the results of accumulated taxonomic richness (in a) or mobile species (in b). Number of plants (at plant level) and beaches (total accumulated) from each biogeographic district are listed at the bottom of each column

Supporting Information Table S4.3). Higher average taxonomic richness of sessile epibionts per plant was observed in the MED and MD compared to CCD and SED ($p < 0.05$) (Figure 2b), as well as in summer compared to winter ($p < 0.05$) (Supporting Information Figure S4.1b). No significant differences were observed in average taxonomic richness of mobile epibionts (Figure 2b and Supporting Information Figure S4.1b, Table S4.3).

Average taxonomic richness of total epibionts per plant varied according to the floating time of beach-cast rafts (Figure 3a and Supporting Information Table S4.4). Taxonomic richness of epibionts decreased with increasing floating time of rafts ($p < 0.05$) (Figure 3a). This same pattern was observed with the accumulated taxonomic richness of epibionts (Chao 2 index) (Figure 3a). Average taxonomic richness of sessile epibionts also varied according to the floating time of the individuals (Supporting Information Table S4.4), showing that taxonomic richness tended to decrease as flotation

time increased ($p < 0.05$), while there were no differences in the case of mobile epibionts (Figure 3b).

3.2 | Co-occurrence of epibiont species

There were 40.4% nonrandom co-occurrences within the total pairs of combinations analysed, of which 56% (22.6% out of the total) were classified as positive and 44% (17.8% out of the total) were negative co-occurrences. The proportion of positive and negative co-occurrences, considering only nonrandom interactions, was not different than that expected by chance ($\chi^2 = 1.14$, $p = 0.211$). In particular, species such as the bivalves *Semimytilus algosus* and *Perumytilus purpuratus*, the polychaete *Phragmatopoma moerchi*, acorn barnacles and the seaweeds *Gelidium linguatum* and *Lessonia spicata* had the highest positive co-occurrences with other epibiont species on stranded individuals of *D. antarctica* (Figure 4). These species are sessile taxa with complex structural morphology that usually appear in dense aggregations of multiple individuals, and are therefore important habitat engineers. On the other hand, the isopod *Limnoria chilensis*, the limpet *Scurria scurra*, crustose calcareous algae and articulated coralline algae had negative co-occurrences with many other epibionts (Figure 4).

3.3 | Comparison of geographic ranges

Twenty-five of the associated species presented rafting ranges overlapping with their literature ranges (RO). Of these species, most were seaweeds with wide literature ranges (e.g. *Macrocystis pyrifera*, *Ceramium virgatum* and *Mazzaella laminarioides*), while eight species were small invertebrates, mainly molluscs (e.g. *S. scurra*, *P. purpuratus*, *Brachidontes granulata*, *S. algosus*, *Hiatella solida*) (Figure 5a). Ten species were found outside their literature ranges, with seaweed epibionts predominating over invertebrates. Seven species were found on beaches south of their known literature ranges (SE), reporting in some cases >200–300 km range extension, such as the seaweeds *Antithamnion densum*, *Gelidium chilense* and *Chaetomorpha firma* and the gastropod *Dendropoma mejillonensis* (Figure 5b). On the other hand, three species were detected on beaches further north than their reported literature ranges (NE), most of them with range extensions of ~100–150 km, although the amphipod *Parawaldeckia kidderi* was found more than 300 km to the north of its literature range (Figure 5c). In general, epibiont species on *D. antarctica* tended to increase towards the southern zone of the study area (37° S–42° S) for all range categories, RO, SE and NE (Supporting Information Figure S4.3).

The frequencies of *D. antarctica* rafts with epibionts outside their benthic ranges differed according to the absence/presence of *Lepas* spp. for SE species (Pseudo- $R^2 = 0.325$; d.f. = 1;12; $p = 0.039$), being higher with the presence of *Lepas* spp. than without them. However, in the case of NE species, there were no differences between rafts with the presence and absence of *Lepas* spp. (Pseudo- $R^2 = 0.091$; d.f. = 1;4; $p = 0.692$) (Figure 6).

Frequencies of raft-associated species on stranded *D. antarctica* found outside of their literature ranges were higher in the presence

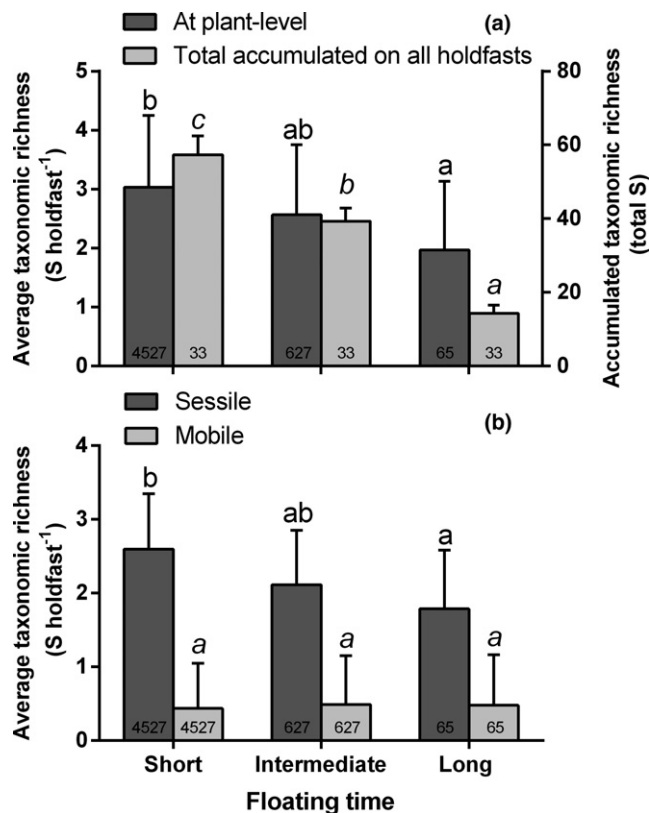


FIGURE 3 Average (mean \pm SD) taxonomic richness of epibionts attached on stranded individuals of *Durvillaea antarctica* on beaches from the continental coast of Chile (28° S–42° S), according to floating time (short, <2 days; intermediate, 2–10 days and long, >10 days). (a) Taxonomic richness at plant level and accumulated per floating time (Chao 2 index). (b) Average taxonomic richness of sessile and mobile epibionts. Letters (a–b–c) above the columns indicate significant differences between floating time categories ($p < 0.05$). Letters in italics correspond to the results of accumulated taxonomic richness (in a) or mobile species (in b). Number of plants (at plant level) and beaches (total accumulated) from each floating time category are listed at the bottom of each column

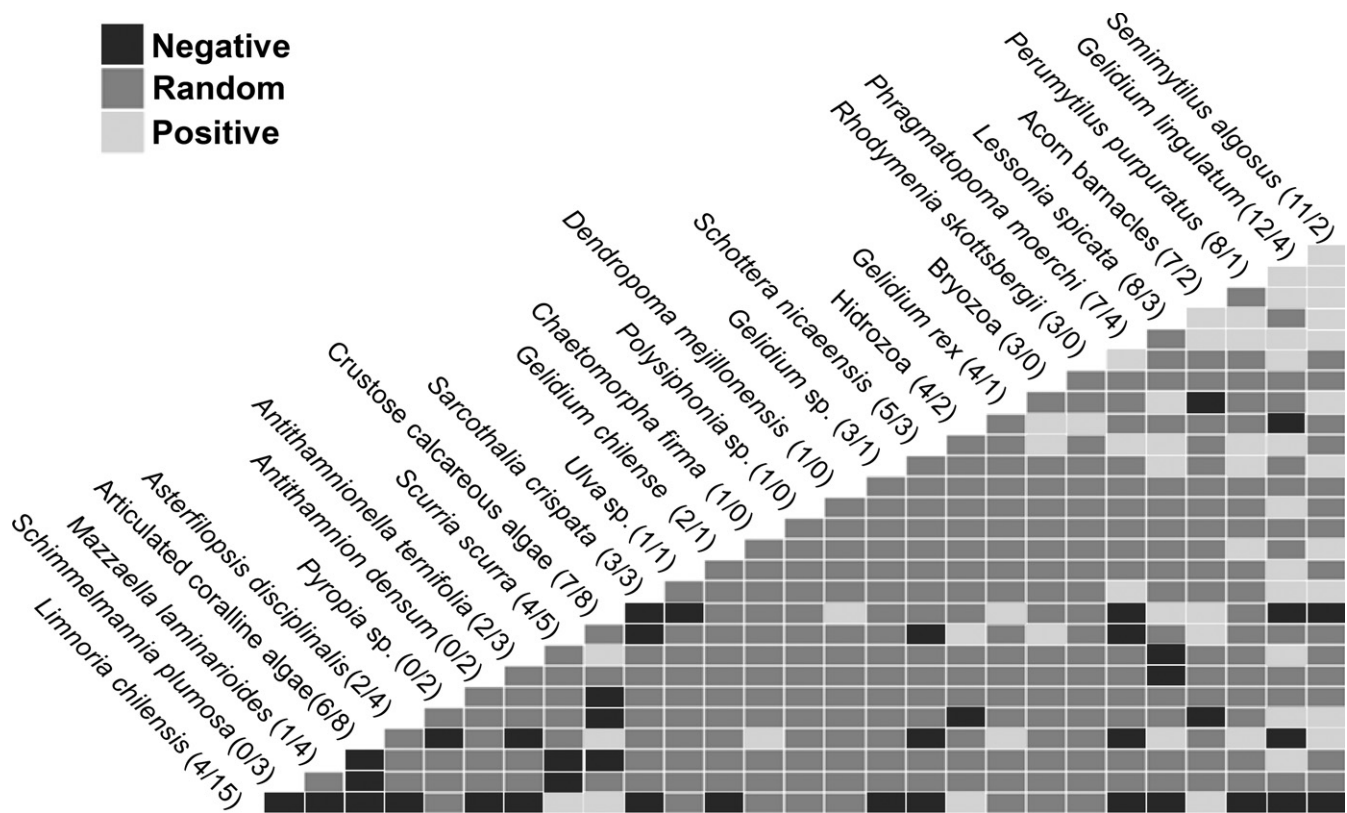


FIGURE 4 Species co-occurrence matrix of frequent epibionts attached on stranded individuals of *Durvillaea antarctica* on beaches from the continental coast of Chile (28° S–42° S), according to positive, negative and random species co-occurrences. The numbers of positive/negative co-occurrences for each species are shown

of epibionts that favour co-occurrences than in the absence of these species, for both SE and NE species (Figure 7a,b, Supporting Information Table S4.5). On the other hand, the percentage of rafts with SE species decreased with the presence of epibiont species that limited co-occurrences (*Limnoria chilensis* and *Scurria scurra*) but this was not the case for NE species (Figure 7c,d, Supporting Information Table S4.5).

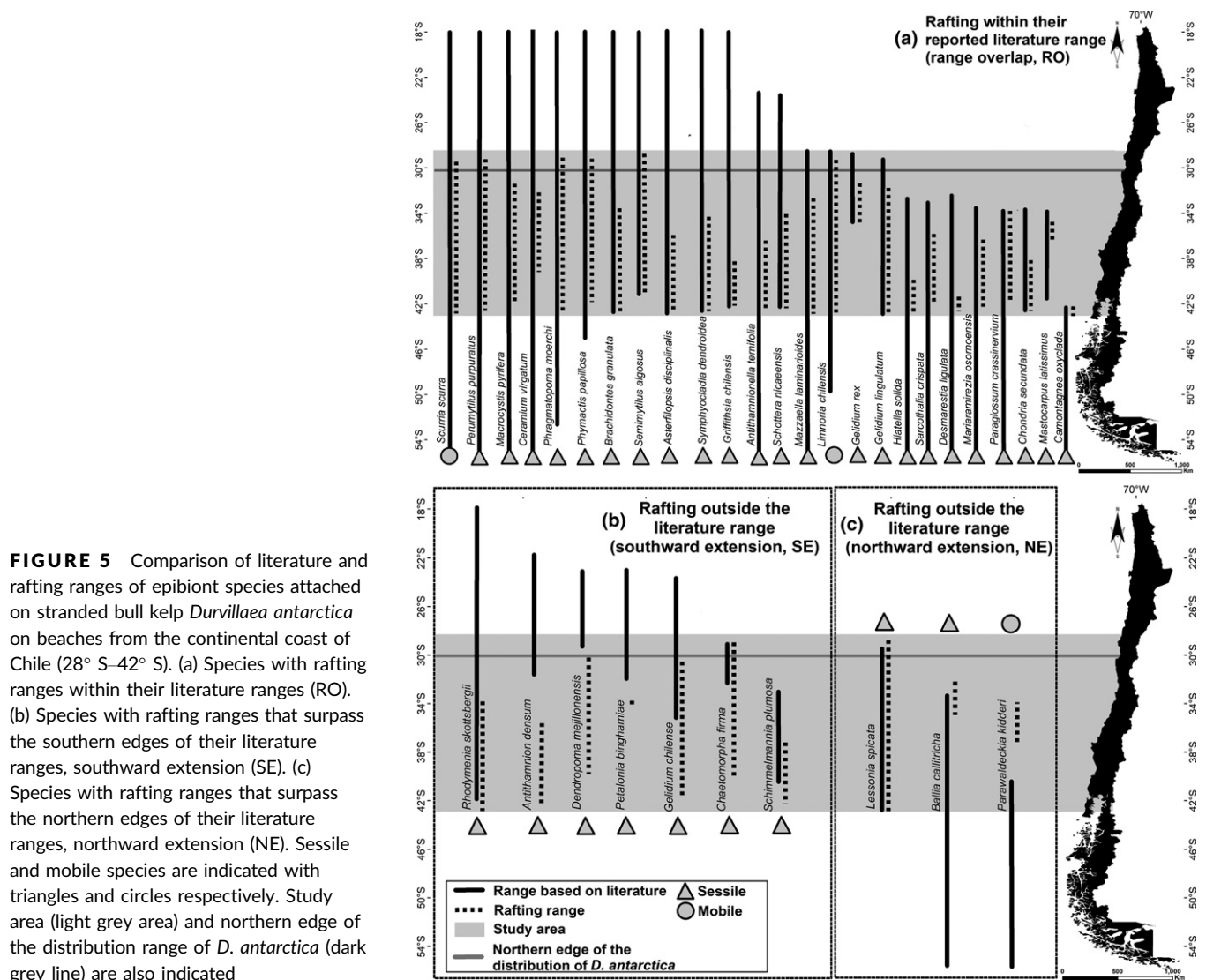
4 | DISCUSSION

Taxonomic richness of the epibiont community on *D. antarctica* rafts varied along the southern-central coast of Chile, particularly among biogeographic districts, coinciding with the genetic structure of the southern bull kelp described for this area (Fraser et al., 2010). Epibionts presented positive and negative co-occurrences with other species, suggesting that these interactions might influence the outcome of long-distance journeys. The results also confirmed that floating bull kelps can carry epibiont species outside of their known literature ranges, apparently with higher dispersal opportunities in areas with more abundant rafts. This suggests that floating seaweeds and the corresponding probability of rafting dispersal can influence the geographic ranges of diverse associated species.

4.1 | Taxonomic richness of the epibiont communities

The number of epibiont species that were transported by floating specimens of *D. antarctica* varied at the plant-level. In general, after detachment from the primary substratum, the amount of epibionts tends to decrease drastically because mobile species with low adhesion capacity are not able to hold onto floating seaweeds or actively evacuate (Gutow et al., 2009, 2015), and mostly sessile species persist on rafts (e.g. stalked barnacles, hydrozoans, bryozoans and seaweeds; Thiel & Gutow, 2005). This coincides with the findings of our study (i.e. low number of epibionts per holdfast, mainly sessile species), although diverse groups have been reported in other studies of floating seaweeds during the pelagic stage (e.g. large fronds of *Ascophyllum*, Gutow et al., 2009; *Sargassum*, Gutow et al., 2015; for an overview see also Thiel & Fraser, 2016).

At the plant-level, total taxonomic richness of epibionts was higher in summer compared to winter. Abundances of rafting organisms fluctuate more seasonally at high latitudes compared to lower latitudes, increasing in summer compared to winter (Thiel & Gutow, 2005). On the other hand, the CCD (28° S–30° S) is the northernmost zone that surpasses the northern edge of the geographic range of *D. antarctica* (~30° S), where lower biomasses and longer floating times of specimens have been observed (López et al., 2017; Tala,



Gómez, Luna-Jorquera, & Thiel, 2013), which can explain the low number of epibionts at plant level.

Sessile epibionts and accumulated richness increased with latitude. These latitudinal trends reflect the biogeographic patterns reported for seaweeds (Santelices & Marquet, 1998) and several invertebrate taxa, such as molluscs (Valdovinos, Navarrete, & Marquet, 2003), peracarids (Fernández, Astorga, Navarrete, Valdovinos, & Marquet, 2009; Rivadeneira, Thiel, González, & Haye, 2011), and polychaetes (Hernández, Moreno, & Rozbaczylo, 2005). Hence, the higher taxonomic richness of epibionts on stranded *D. antarctica* from southern districts can be explained with the increasing taxonomic richness of benthic biota (mainly sessile) towards the south of our study area.

The decreasing epibiont diversity with increasing floating time of *D. antarctica* rafts suggests that few species are able to withstand long periods afloat. In general, species inhabiting the lower intertidal or shallow subtidal zone (such as *D. antarctica* and its epibiont community) tend to have less resistance to environmental stress (e.g. at the sea surface) than species that live in the mid-upper intertidal

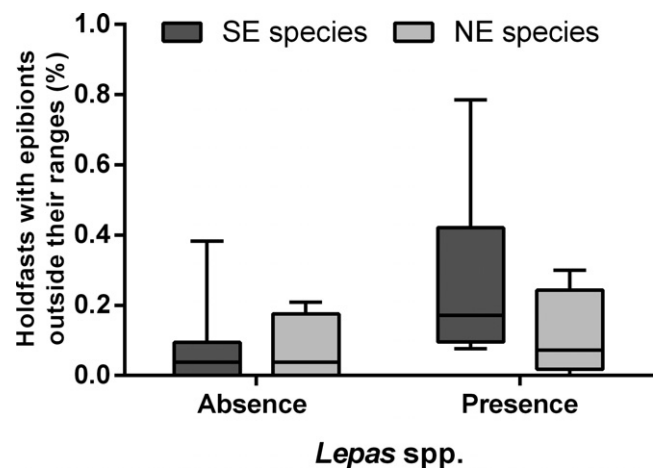


FIGURE 6 Box plot of percentages of stranded individuals of *Durvillaea antarctica* with epibionts outside their literature ranges according to the absence and presence of *Lepas* spp. for SE (southward extension) and NE species (northward extension) on beaches along the continental coast of Chile (28° S–42° S). Horizontal lines represent the median; boxes, the interquartile range; whiskers, 1.5x of interquartile range

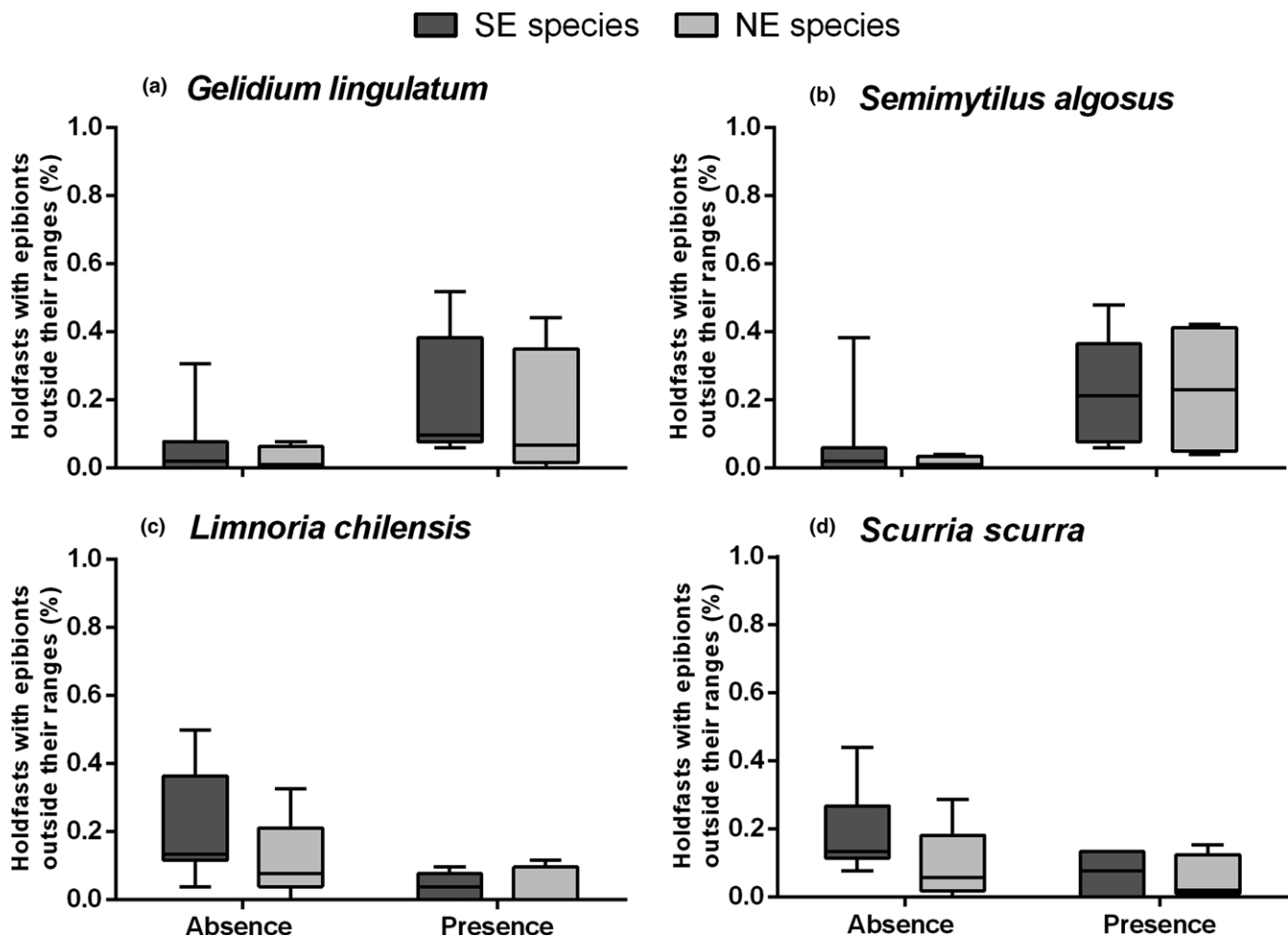


FIGURE 7 Box plot of percentages of stranded individuals of *Durvillaea antarctica* with epibionts outside their literature ranges (% per beach) according to the absence and presence of epibiont species with positive co-occurrences, (a) *Gelidium lingulatum* and (b) *Semimytilus algosus*, and epibiont species with negative co-occurrences, (c) *Limnoria chilensis* and (d) *Scurria scurra* for SE (southward extension) and NE species (northward extension) on beaches along the continental coast of Chile (28° S–42° S). Horizontal lines represent the median; boxes, the interquartile range; whiskers, 1.5x of interquartile range

zone (e.g. Flores-Molina et al., 2014; Gómez & Huovinen, 2011). Also, taxonomic richness of epibionts was lower on rafts with long floating times in the northern (mainly in summer) than in the southern districts. This is congruent with the latitudinal and seasonal gradient of stressful conditions that suppress the persistence of floating seaweeds at the sea surface (Tala, Velásquez, Mansilla, Macaya, & Thiel, 2016; Tala et al., 2013). Hence, our findings support the hypothesis that some raft-associated species are lost with increasing floating time. Future studies should focus on the functional responses of raft-associated species along a latitudinal gradient, complemented with ecophysiological experiments under controlled floating conditions.

4.2 | Co-occurrences of epibiont species

Several positive and negative co-occurrences among epibionts of *D. antarctica* were observed within single bull kelp rafts. Ecosystem engineers that generate habitat for other epibionts (e.g. structural

complexity, refuges, large size), such as the turf-forming seaweed *Gelidium lingulatum* (González, Stotz, Toledo, Jorquera, & Romero, 1991), the canopy-forming kelp *Lessonia spicata* (Westermeier, Muller, Gómez, Rivera, & Wenzel, 1994), mussels (*Perumytilus purpuratus* and *Semimytilus algosus*) that form dense three-dimensional matrices (Prado & Castilla, 2006), and the reef-building tube worm *Phragmatopoma moerchi* (Sepúlveda, Moreno, & Carrasco, 2003) presented many positive interactions. On the other hand, mobile species that open cavities in the holdfast, thereby destroying attachment surfaces and diminishing the available area for other epibionts during rafting journeys, such as the boring isopod *Limnoria chilensis* (Thiel, 2003) and the excavating limpet *Scurria scurra* (Vásquez, Veliz, & Pardo, 2001), were negatively correlated with other rafting species.

Epibiont species with high number of positive co-occurrences with other species (e.g. *Gelidium lingulatum* and *Semimytilus algosus*) were common on stranded specimens in the southern districts suggesting that they contribute to the high richness of rafting species in these areas and facilitate their range expansions. In the case of



epibionts with mostly negative co-occurrences, there was no clear latitudinal pattern, although they were frequent (e.g. *Limnoria chilensis*) on stranded individuals with indications of longer floating times. This could indicate that the presence of these species might cause the disappearance of other epibionts during prolonged rafting journeys. Our results are the first to suggest that biological interactions within a raft may facilitate or suppress the persistence of other epibiont species during long-distance dispersal, thereby potentially affecting immigration to other areas along a latitudinal gradient. It is also possible that our findings are influenced by biotic interactions that occurred prior to the detachment of bull kelp from the rocks, but there are a number of indications that support our interpretation. Several previous studies had shown that epibiont communities on benthic holdfasts of *D. antarctica* are very different (Edgar & Burton, 2000; Santelices et al., 1980) from those observed in the pelagic stage (our study), with a much lower proportion of mobile species (e.g. snails, crabs, sea urchins) in floating kelps. Furthermore, rapid emigration immediately after detachment has been reported in other studies (e.g. Gutow et al., 2009; Miranda & Thiel, 2008) where many mobile organisms abandon holdfasts during the first minutes after the detachment of buoyant kelps. Indeed, herein we found a high proportion of sessile organisms in the stranded kelps, suggesting that important changes had occurred after detachment and that the observed results are the outcome of interactions during the (possibly short) rafting voyages.

4.3 | Travelling outside of their geographic ranges

Most rafting epibionts were found within their known literature ranges (i.e. RO species). These species are characterized by wide geographic ranges and in the case of invertebrates, many of them have long planktonic larval phases (see Supporting Information Table S3.1). On the other hand, all species that presented extensions of their ranges are organisms that have low autonomous dispersal ability, which suggests that rafting dispersal on floating seaweeds could be an effective mechanism of dispersal. Range extensions tend to be wider towards the southern edge of the ranges (i.e. SE species), where there are abundant floating kelp supplies and environmental conditions at the sea surface are less severe (i.e. lower temperature and solar radiation), facilitating raft persistence and return to the coast (López et al., 2017; Tala et al., 2016). In contrast, few species showed extension at the northward edge of their ranges (i.e. NE species) and these extensions were smaller than in SE species. This is interesting because this zone coincides with the biogeographic break at 30° S (Camus, 2001), which corresponds to the northern edge of benthic populations of *D. antarctica* (Hoffmann & Santelices, 1997). This area is characterized by oceanographic characteristics (i.e. local current and winds) that affect dispersal and recruitment of several benthic invertebrates (e.g. Broitman, Navarrete, Smith, & Gaines, 2001), and also has consequences for the population connectivity of species with low dispersal ability (e.g. Haye et al., 2014). Therefore, our results support the hypothesis that range extensions of raft-associated

species are more common and wider towards the south of their known literature ranges. Moreover, our results suggest that rafting dispersal by floating seaweeds might have contributed to the recent range expansion of the introduced seaweed *Schottera nicaeensis* (Villaseñor-Parada, Pauchard, & Macaya, 2014) in the southern zone (37° S–42° S).

Epibionts found outside their literature ranges showed a slight tendency to be found on stranded bull kelps with indications of prolonged floating times. López et al. (2017) showed that the presence and size of *Lepas* spp. attached to beach-cast rafts of *D. antarctica* varies strongly along the latitudinal gradient among biogeographic districts, being more frequent at 28° S–33° S and 37° S–42° S, and less frequent from 33° S to 37° S. These geographic patterns agree with the range extensions evidenced in our study for SE and NE species. This suggests that long-distance dispersal episodes may be more frequent in certain areas (e.g. 37° S–42° S), which probably explains higher range extensions in southern areas, whereas rafts in northern districts (CCD and SED) usually have depressed photosynthetic responses and protective mechanisms (Tala et al., 2013), which limits their survival at the sea surface and would explain the shorter range extensions in those areas. Moreover, higher the presence of epibionts with positive co-occurrences on rafts beyond the literature ranges and lower occurrence of epibiont species with negative co-occurrences in these expansions suggest the importance of biotic interactions during long-distance rafting dispersal that facilitate or restrict successful immigration to other areas. Lastly, our results suggest the first example of a habitat cascade (sensu Thomsen & Wernberg, 2014) as a mechanism for range extensions. Holdfasts of floating bull kelps provide habitat to sessile taxa (e.g. mussels) that then generate habitat for additional epibiont species, thereby facilitating their long-distance dispersal.

5 | CONCLUSION AND OUTLOOK

Our study strongly indicates that some species are frequently being dispersed via bull kelp rafts, adding support to phylogeographic studies, which had shown long-distance connectivity for peracarid populations from New Zealand and Chile (e.g. *L. chilensis*, Nikula et al., 2010; *P. kidderi*, Haye, Varela, & Thiel, 2012). However, in other cases, our study actually provides no support for frequent rafting dispersal—this is, for example, the case for the snail *Diloma nigerrima*, a species that has genetic similarities between populations of New Zealand and Chile (Donald, Kennedy, & Spencer, 2005), but that was not observed on any of the stranded kelps examined in our study. Similar examples are the sea slugs from the genus *Onchidella* (Cumming, Nikula, Spencer, & Waters, 2014) and the seaweed *Gracilaria chilensis* (Guillemin, Valero, Faugeton, Nelson, & Destombe, 2014), both of which were also not found on our stranded holdfasts. Finally, their high frequency of occurrence on stranded *D. antarctica* holdfasts suggests that in some species with long-lived autonomous dispersal stages (i.e. planktonic larval



stage for more than 10 days), such as the mytilid mussels *S. algosus* and *P. purpuratus*, the limpet *S. scurra* and the polychaete *P. moerchi* (Haye et al., 2014; Trovant, Orensanz, Ruzzante, Stotz, & Basso, 2015), rafting on seaweeds might be a complementary dispersal mechanism (in addition to larval dispersal) that could also affect their population connectivity.

In summary, our study shows that rafting dispersal by floating seaweeds is a mechanism that could contribute to the structuring of the geographic ranges of epibiont species, particularly those with low autonomous dispersal ability. However, these range expansions of raft-associated species are strongly influenced by the availability of rafts, environmental conditions at the sea surface and local oceanographic features that affect successful immigration to other areas. Predicted climate change impacts on floating seaweeds and their epibiont communities (i.e. changes in supplies, transport and permanence of rafts; Macreadie, Bishop, & Booth, 2011) should also be considered in future studies.

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REFERENCES

- Broitman, B. R., Navarrete, S. A., Smith, F., & Gaines, S. D. (2001). Geographic variation of southeastern Pacific intertidal communities. *Marine Ecology Progress Series*, 224, 21–34. <https://doi.org/10.3354/meps224021>
- Camus, P. A. (2001). Biogeografía marina de Chile continental. *Revista Chilena de Historia Natural*, 74, 587–617.
- Chao, A., & Lee, S. M. (1992). Estimating the number of classes via sample coverage. *Journal of the American Statistical Association*, 87, 210–217. <https://doi.org/10.1080/01621459.1992.10475194>
- Clarke, K. R., Gorley, R. N., Somerfield, P. J., & Warwick, R. M. (2014). *Change in marine communities: An approach to statistical analysis and interpretation* (3rd ed.). Plymouth, UK: PRIMER-E.
- Cumming, R. A., Nikula, R., Spencer, H. G., & Waters, J. M. (2014). Trans-oceanic genetic similarities of kelp-associated sea slug populations: Long-distance dispersal via rafting? *Journal of Biogeography*, 41, 2357–2370. <https://doi.org/10.1111/jbi.12376>
- Donald, K. M., Kennedy, M., & Spencer, H. G. (2005). Cladogenesis as the result of long-distance rafting events in South Pacific topshells (Gastropoda, Trochidae). *Evolution*, 59, 1701–1711. <https://doi.org/10.1111/j.0014-3820.2005.tb01819.x>
- Duarte, C., Jaramillo, E., Contreras, H., Acuña, K., & Navarro, J. M. (2009). Importance of macroalgae subsidy on the abundance and population biology of the amphipod *Orchestoidea tuberculata* (Nicolet) in sandy beaches of south central Chile. *Revista de Biología Marina y Oceanografía*, 44, 691–702.
- Edgar, G. J., & Burton, H. R. (2000). The biogeography of shallow-water macrofauna at Heard Island. In M. R. Banks & M. J. Brown (Eds.), *Heard Island papers. Papers and proceedings of the Royal Society of Tasmania* (pp. 23–26). Hobart, Australia: University of Tasmania.
- Fernández, M., Astorga, A., Navarrete, S. A., Valdovinos, C., & Marquet, P. A. (2009). Deconstructing latitudinal species richness patterns in the ocean: Does larval development hold the clue? *Ecology Letters*, 12, 601–611. <https://doi.org/10.1111/j.1461-0248.2009.01315.x>
- Flores-Molina, M. R., Thomas, D., Lovazzano, C., Núñez, A., Zapata, J., Kumar, M., ... Contreras-Porcía, L. (2014). Desiccation stress in intertidal seaweeds: Effects on morphology, antioxidant responses and photosynthetic performance. *Aquatic Botany*, 113, 90–99. <https://doi.org/10.1016/j.aquabot.2013.11.004>
- Fraser, C. I., Thiel, M., Spencer, H. G., & Waters, J. M. (2010). Contemporary habitat discontinuity and historic glacial ice drive genetic divergence in Chilean kelp. *BMC Evolutionary Biology*, 10, 203. <https://doi.org/10.1186/1471-2148-10-203>
- Gómez, I., & Huovinen, P. (2011). Morpho-functional patterns and zonation of South Chilean seaweeds: The importance of photosynthetic and bio-optical traits. *Marine Ecology Progress Series*, 422, 77–91. <https://doi.org/10.3354/meps08937>
- González, A. V., Beltrán, J., Flores, V., & Santelices, B. (2015). Morphological convergence in the inter-herdfast coalescence process among kelp and kelp-like seaweeds (*Lessonia*, *Macrocystis*, *Durvillaea*). *Phycologia*, 54, 283–291. <https://doi.org/10.2216/14-105.1>
- González, S., Stotz, W., Toledo, P., Jorquera, M., & Romero, M. (1991). Utilización de diferentes microambientes del intermareal como lugares de asentamiento por *Fissurella* spp (Gastropoda : Prosobranchia) (Palo Colorado, Los Vilos, Chile). *Revista de Biología Marina y Oceanografía*, 26, 325–338.
- Griffith, D. M., Veech, J. A., & Marsh, C. J. (2016). Cooccur: Probabilistic species co-occurrence analysis in R. *Journal of Statistical Software*, 69, 1–17.
- Guillemin, M. L., Valero, M., Faugeron, S., Nelson, W., & Destombe, C. (2014). Tracing the trans-pacific evolutionary history of a domesticated seaweed (*Gracilaria chilensis*) with archaeological and genetic data. *PLoS ONE*, 9, e114039. <https://doi.org/10.1371/journal.pone.0114039>
- Gutow, L., Beermann, J., Buschbaum, C., Rivadeneira, M. M., & Thiel, M. (2015). Castaways can't be choosers - Homogenization of rafting assemblages on floating seaweeds. *Journal of Sea Research*, 95, 161–171. <https://doi.org/10.1016/j.seares.2014.07.005>
- Gutow, L., Giménez, L., Boos, K., & Saborowski, R. (2009). Rapid changes in the epifaunal community after detachment of buoyant benthic macroalgae. *Journal of the Marine Biological Association of the United Kingdom*, 89, 323–328. <https://doi.org/10.1017/S0025315408002658>
- Haye, P. A., Segovia, N. I., Muñoz-Herrera, N. C., Gálvez, F. E., Martínez, A., Meynard, A., ... Faugeron, S. (2014). Phylogeographic structure in benthic marine invertebrates of the southeast Pacific coast of Chile with differing dispersal potential. *PLoS ONE*, 9, e88613. <https://doi.org/10.1371/journal.pone.0088613>
- Haye, P. A., Varela, A. I., & Thiel, M. (2012). Genetic signatures of rafting dispersal in algal-dwelling brooders *Limnoria* spp. (Isopoda) along the SE Pacific (Chile). *Marine Ecology Progress Series*, 455, 111–122. <https://doi.org/10.3354/meps09673>
- Hernández, C. E., Moreno, R. A., & Rozbaczylo, N. (2005). Biogeographical patterns and Rapoport's rule in southeastern Pacific benthic polychaetes of the Chilean coast. *Ecography*, 28, 363–373. <https://doi.org/10.1111/j.0906-7590.2005.04013.x>

- Hoffmann, A., & Santelices, B. (1997). *Flora marina de Chile Central*. Santiago de Chile, Chile: Ediciones Universidad Católica de Chile.
- Lester, S. E., Ruttenberg, B. I., Gaines, S. D., & Kinlan, B. P. (2007). The relationship between dispersal ability and geographic range size. *Ecology Letters*, *10*, 745–758. <https://doi.org/10.1111/j.1461-0248.2007.01070.x>
- López, B. A., Macaya, E. C., Tala, F., Tellier, F., & Thiel, M. (2017). The variable routes of rafting: Stranding dynamics of floating bull kelp *Durvillaea antarctica* (Fuecales, Phaeophyceae) on beaches in the SE Pacific. *Journal of Phycology*, *53*, 70–84. <https://doi.org/10.1111/jpy.12479>
- Macaya, E. C., López, B., Tala, F., Tellier, F., & Thiel, M. (2016). Float and raft: Role of buoyant seaweeds in the phylogeography and genetic structure of non-buoyant associated flora. In Z. M. Hu & C. I. Fraser (Eds.), *Seaweed phylogeography* (pp. 97–130). Dordrecht, The Netherlands: Springer. <https://doi.org/10.1007/978-94-017-7534-2>
- Macreadie, P. I., Bishop, M. J., & Booth, D. J. (2011). Implications of climate change for macrophytic rafts and their hitchhikers. *Marine Ecology Progress Series*, *443*, 285–292. <https://doi.org/10.3354/meps09529>
- Miranda, L., & Thiel, M. (2008). Active and passive migration in boring isopods *Limnoria* spp. (Crustacea, Peracarida) from kelp holdfasts. *Journal of Sea Research*, *60*, 176–183. <https://doi.org/10.1016/j.seares.2008.06.002>
- Nikula, R., Fraser, C. I., Spencer, H. G., & Waters, J. M. (2010). Circumpolar dispersal by rafting in two subantarctic kelp-dwelling crustaceans. *Marine Ecology Progress Series*, *405*, 221–230. <https://doi.org/10.3354/meps08523>
- Nikula, R., Spencer, H. G., & Waters, J. M. (2013). Passive rafting is a powerful driver of transoceanic gene flow. *Biology Letters*, *9*, 20120821.
- Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., ... Wagner, H. (2017). Vegan: Community ecology package. R package version 2.4-4. Retrieved from <http://CRAN.R-project.org/package=vegan>.
- Prado, L., & Castilla, J. C. (2006). The bioengineer *Perumytilus purpuratus* (Mollusca: Bivalvia) in central Chile: Biodiversity, habitat structural complexity and environmental heterogeneity. *Journal of the Marine Biological Association of the United Kingdom*, *86*, 417–421. <https://doi.org/10.1017/S0025315406013282>
- R Development Core Team. (2017). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from <http://www.r-project.org/>.
- Rivadeneira, M. M., Thiel, M., González, E. R., & Haye, P. A. (2011). An inverse latitudinal gradient of diversity of peracarid crustaceans along the Pacific Coast of South America: Out of the deep south. *Global Ecology and Biogeography*, *20*, 437–448. <https://doi.org/10.1111/j.1466-8238.2010.00610.x>
- Santelices, B., Castilla, J. C., Cancino, J., & Schmiede, P. (1980). Comparative ecology of *Lessonia nigrescens* and *Durvillaea antarctica* (Phaeophyta) in central Chile. *Marine Biology*, *59*, 119–132. <https://doi.org/10.1007/BF00405461>
- Santelices, B., & Marquet, P. A. (1998). Seaweeds, latitudinal diversity patterns, and Rapoport's rule. *Diversity and Distributions*, *4*, 71–75. <https://doi.org/10.1046/j.1472-4642.1998.00005.x>
- Sepúlveda, R. D., Moreno, R. A., & Carrasco, F. D. (2003). Diversidad de macroinvertebrados asociados a arrecifes de *Phragmatopoma moerchi* Kinberg, 1867 (Polychaeta: Sabellariidae) en el intermareal rocoso de Cocholgué, Chile. *Gayana (Concepción)*, *67*, 45–54.
- Stoner, A. W., & Greening, H. S. (1984). Geographic variation in the macrofaunal associates of pelagic *Sargassum* and some biogeographic implications. *Marine Ecology Progress Series*, *20*, 185–192. <https://doi.org/10.3354/meps020185>
- Tala, F., Gómez, I., Luna-Jorquera, G., & Thiel, M. (2013). Morphological, physiological and reproductive conditions of rafting bull kelp (*Durvillaea antarctica*) in northern-central Chile (30°S). *Marine Biology*, *160*, 1339–1351. <https://doi.org/10.1007/s00227-013-2186-8>
- Tala, F., Penna-Díaz, M. A., Luna-Jorquera, G., Rothäusler, E., & Thiel, M. (2017). Daily and seasonal changes of photobiological responses in floating bull kelp *Durvillaea antarctica* (Chamisso) Hariot (Fuecales: Phaeophyceae). *Phycologia*, *56*, 271–283. <https://doi.org/10.2216/16-93.1>
- Tala, F., Velásquez, M., Mansilla, A., Macaya, E. C., & Thiel, M. (2016). Latitudinal and seasonal effects on short-term acclimation of floating kelp species from the South-East Pacific. *Journal of Experimental Marine Biology and Ecology*, *483*, 31–41. <https://doi.org/10.1016/j.jembe.2016.06.003>
- Thiel, M. (2003). Reproductive biology of *Limnoria chilensis*: Another boring peracarid species with extended parental care. *Journal of Natural History*, *37*, 1713–1726. <https://doi.org/10.1080/00222930210125416>
- Thiel, M., & Fraser, C. I. (2016). The role of floating plants in dispersal of biota across habitats and ecosystems. In E. Olafsson (Ed.), *Marine macrophytes as foundation species* (pp. 76–99). Boca Raton, FL: CRC Press, Taylor & Francis Group. <https://doi.org/10.4324/9781315370781>
- Thiel, M., & Gutow, L. (2005). The ecology of rafting in the marine environment. II. The rafting organisms and community. *Oceanography and Marine Biology: An Annual Review*, *43*, 279–418. <https://doi.org/10.1201/CRCOCEMARBIO>
- Thiel, M., & Vásquez, J. A. (2000). Are kelp holdfasts islands on the ocean floor? Indication for temporarily closed aggregations of peracarid crustaceans. *Hydrobiologia*, *440*, 45–54. <https://doi.org/10.1023/A:1004188826443>
- Thomsen, M. S., & Wernberg, T. (2014). On the generality of cascading habitat-formation. *Proceedings of the Royal Society of London B, Biological Sciences*, *281*, 20131994. <https://doi.org/10.1098/rspb.2013.1994>
- Trovant, B., Orensanz, J. M., Ruzzante, D. E., Stotz, W., & Basso, N. G. (2015). Scorched mussels (Bivalvia: Mytilidae: Brachidontinae) from the temperate coasts of South America: Phylogenetic relationships, trans-Pacific connections and the footprints of Quaternary glaciations. *Molecular Phylogenetics and Evolution*, *82*, 60–74. <https://doi.org/10.1016/j.ympev.2014.10.002>
- Valdovinos, C., Navarrete, S. A., & Marquet, P. A. (2003). Mollusk species diversity in the Southeastern Pacific: Why are there more species towards the pole? *Ecography*, *26*, 139–144. <https://doi.org/10.1034/j.1600-0587.2003.03349.x>
- Vandendriessche, S., Vincx, M., & Degraer, S. (2007). Floating seaweed and the influences of temperature, grazing and clump size on raft longevity - A microcosm study. *Journal of Experimental Marine Biology and Ecology*, *343*, 64–73. <https://doi.org/10.1016/j.jembe.2006.11.010>
- Vásquez, J. A., Veliz, D., & Pardo, L. M. (2001). Biodiversidad de macroinvertebrados bajo las grandes algas. In K. Alveal & T. Antezana (Eds.), *Sustentabilidad de la biodiversidad. Un problema actual: Bases científico técnicas, teorizaciones y proyecciones* (pp. 293–308). Concepción: Universidad de Concepción.
- Veech, J. A. (2014). The pairwise approach to analysing species co-occurrence. *Journal of Biogeography*, *41*, 1029–1035. <https://doi.org/10.1111/jbi.12318>
- Villaseñor-Parada, C., Pauchard, A., & Macaya, E. (2014). Expansión del área de distribución de la macroalga introducida *Schottera nicaeensis* (Rhodophyta: Gigartinales) en la costa chilena: ¿evidencia de una invasión? *Boletín de la Red Latinoamericana para el Estudio de Especies Invasoras*, *4*, 19–27.



Westermeier, R., Muller, D. G., Gómez, I., Rivera, P., & Wenzel, H. (1994). Population biology of *Durvillaea antarctica* and *Lessonia nigrescens* (Phaeophyta) on the rocky shores of southern Chile. *Marine Ecology Progress Series*, 110, 187–194. <https://doi.org/10.3354/meps110187>

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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