



The first phycopathological atlas in Latin America unveils the underdocumentation of algal pathogens

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ABSTRACT

To date, the biodiversity of disease-causing agents in algae has been poorly investigated. This information however is particularly relevant, as outbreaks are repeatedly reported in mariculture facilities or commercial wild stocks, with no available baselines to compare with. Algal pathogens identified in Latin America are few; information is scattered and mostly unknown for regional aquacultural actors such as farmers, seaweed gatherers, conservation biologists and policymakers. In this work, we reviewed all the pathogens described for algae in Latin America, including their taxonomy, macro and microscopic symptoms, aetiology, habitat and reported distribution in this region. Furthermore, we included new records obtained in 2020–2022 in the Southeastern Pacific, and the results of a screen for viruses on kelp gametophytes from a regional germplasm including south Pacific and Atlantic strains. Only nine countries have described algal pathogens so far. The Southeast Pacific (Chilean coast) concentrates the largest number of records and correspond to endophytic algae of different taxa (34 %), viruses (21 %) and protistan pseudofungi (20 %). In our 2020–2022 sampling campaigns, 33 new records were reported for Latin America, which constitutes 15 % of the total records for the region. Overall, unbalanced track records were detected at geographical (e.g. country), temporal (year), diagnosis type and outbreak level, possibly due to scattered and unsystematic sampling efforts. Our results show that pathogens remain cryptic threats for seaweed-related human activities. We anticipate that as the sampling effort increases, algal pathogen records will also increase in number and importance, in proportions comparable to other ecologically and commercially relevant aquatic resources.

1. Introduction

Algal pathogens play a pivotal role in shaping the ecological dynamics of aquatic environments, influencing the health and diversity associated to primary productivity [1]. These microscopic assailants,

ranging from viruses and bacteria to fungi and protists [2], represent key actors in the intricate web of interactions within ecosystems. They contribute to the regulation of algal populations by causing diseases, which can lead to shifts in community composition and abundance [3], the repercussions of which may cascade through entire ecosystems. For

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instance, pathogen-induced changes in algal community structure can affect nutrient cycling, alter the availability of resources, and impact the trophic relationships within aquatic food webs [4]. In case of anthropogenic ecosystem disruptions, algal diseases may represent a significant ecological concern within aquatic ecosystems, exerting profound impacts on the delicate balance of these environments, with ecological consequences beyond the affected organisms [5]. As such, understanding the ecological roles and consequences of algal pathogens is essential for comprehending the broader implications of disease dynamics in aquatic ecosystems and underscores the need for holistic approaches to ecosystem management and conservation [6]. Latin America (hereafter LATAM; as the 33 countries defined by the UN ECLAC) is one of the regions with the least knowledge on algal pathogens, despite having an enormous diversity of algae. This lack of knowledge is perceived as one of the major gaps affecting the sustainability of algal-related economic activities such as fisheries and aquaculture [7].

Beyond their ecological aspects, pathogens are one of the most relevant biosecurity problems in algal aquaculture [7,8]. For LATAM algae, very few pathogens (*sensu stricto*) have been reported in the wild [9,10], and even less in commercial stocks [11]. In comparison, >65 disease aetiological agents are associated with farmed eucheumatoids (*Eucheuma* and *Kappaphycus* spp.), Bangiales (*Pyropia* and *Porphyra* spp.) and kelps (e.g. *Saccharina japonica*, *Undaria pinnatifida*) in Asia, where aquaculture is more widespread [8,12]. This track record still seems deficient, nevertheless, when compared with agronomy or animal aquaculture. The first reports of pathogen-driven algal diseases were compiled in the early 20th century: an exhaustive review produced at the time was limited in scope to so-called phycomycetes, due to the technology available at the time (e.g. optical microscopy) [13]. Since then, most novel records have been predominantly accidental findings from aquaculture trials or ecological studies, instead of results from targeted epidemiological campaigns [14]. In Asia, new species of algal pathogens are currently discovered almost every year, with an algal aquaculture industry starting to struggle due to disease outbreaks [15]. Some of these epidemics are likely linked with the consequences of domestication, such as reduction of genetic variation or overuse of clonal varieties [16]. In comparison to other regions of the world, reports of algal diseases and pests remain scarce in LATAM [14]. Yet, it is well-known that algal diseases are not only ubiquitous in aquatic systems [9,17], but also significant bottom-up regulators of algal wild populations [2,18]. Hence, a broad diversity of algal pathogens is expected to occur in healthy, as well as anthropogenised ecosystems [19].

Algal cultivation is normally perceived to be environmentally friendly, as algae may contribute to reduce nutrients (e.g. carbon dioxide and nitrogen nutrients) in eutrophicated systems, and instead supply oxygen [20]. However, it is less documented that, as any human activity, algal aquaculture might also incur new threats for humans and the environment. The known fingerprints of seaweed aquaculture involve physical, biological and aesthetic impacts [21], being disease outbreaks and pathogen dissemination thereafter one of the most relevant [22,23]. Diseases may be encouraged from and within facilities by the introduction of new susceptible host for native diseases or by outplanting diseased stocks in aquaculture facilities, facilitating cross-infections between neighbouring wild populations and farmed specimens [4]. Alternatively, farmed seaweeds can be reservoir of cryptic pathogens even from biobanks (e.g. lysogenic phaeoviruses in kelps [24]), which without proper understanding on their biological cycles may be transferred to local species. Furthermore, these local species may act as intermediate hosts [25,26], hosting temporarily pathogens that later on may be threat for both farmed specimens and/or wild species.

Now that public and private interests have started to shift toward algal exploitation globally [27], the potential hazards need evaluation, in order to develop a resilient and sustainable industry [28]. These assessments need to include the potential disease risks of both native and farmed species cultivation, as they have demonstrated to be a relevant reservoir for aquacultural-relevant pathogens [23]. With the aim to

further inform aquaculture biosecurity practices that are just starting to be implemented in LATAM regional policies [7], we present here the first baseline dataset of algal diseases in LATAM, aiming to highlight the lack of knowledge on this matter and the repercussions that this deficit may have in the incipient algaculture in the region. For this purpose, we gathered information already published in regional and worldwide repositories, we included our own unpublished data from Chilean records and also screened a national kelp germplasm for virus presence, in order to present the most up-to-date checklist of LATAM algal pathogens. This dataset also includes an atlas (e.g. compendium of maps), to differentiate hotspots of micro- and macroalgal pathogens from areas with lower pathogen characterization.

2. Materials and methods

2.1. Literature review

We carried out an extensive search of Web of Science (WoS) articles and regional journals (available at SCIELO network), as well as Google Scholar, looking for reported diseases in micro- and macroalgae from marine and freshwater environments. Specifically, we queried keywords associated with the host (microalgae, macroalgae, algae, seaweed, brown/red/green seaweed, diatom dinoflagellate etc.) combined with keywords associated with pathogen types (viruses, bacteria, fungi, protists, algal endophytes, algal parasites) and their putative interaction (pathogen, parasite, infection, disease), plus locations within Latin America (33 countries according to UN ECLAC; www.cepal.org). We only consider publications where pathogens were associated to a disease (s), where macroscopic (such as malformations, gall formation, necrosis, bleaching, overpigmentation etc.) and/or microscopic (hypertrophy, hyperplasia, cell wall thickening, intracellular infection) symptoms reported were clearly specified. For such reason, in this review we did not consider epiphytes (neither alga or bacteria) as diseases, as in most cases the pathogenic nature of such interactions was not clearly documented in the studies. We classified every article/report by host and pathogen taxonomy, pathogen type (from viruses to algal parasites; in case of cyanobacterial endophytes they were considered as bacteria), and the impact of the respective disease within host population(s): asymptomatic (not recognizable by naked-eye and microscopically), punctual finding (e.g. one to few diseased individuals) and outbreak (significant proportion of a population infected). Furthermore, we identified the country(ies), habitat type (freshwater or marine), locality(ies) name(s), geographical coordinates and date(s) for the record(s) (at least the year). When the latter two were not clearly stated in the respective study, we included the year of publication and an approximate coordinate based on the name of the locality.

2.2. Sampling

In addition to reviewing the literature for reports of algal pathogens in LATAM, we carried out sampling campaigns in Southern Chile to extend the current known baseline of algal diseases in LATAM. We collected representative macroalgae (a.k.a. those with coverage >1 % or identifiable by naked eye) in the intertidal and upper subtidal (up to 2 m, five replicates per species, one sample per independent square meter) (Full list of collected seaweeds in [Suppl. Table 1](#)). The sampling was performed prioritizing symptomatic individuals and thallus sections (e.g. bearing galls, warts or discolouration), although in case they were not easily-identifiable, we sampled healthy-looking individuals instead. Such specimens were stored in sterile sealable bags inside cooling boxes, before being transported to the lab for inspection. In this article we refer only to symptomatic and diseased individuals from such samplings.

Since there is increasing body of evidence of high prevalence of phaeoviruses in brown seaweeds and protocols for barcoding them are available [29], asymptomatic gametophytes from a kelp germplasm available at the Universidad Austral de Chile were stored in RNAlater®

Table 1

Checklist of LATAM algal diseases and their symptoms, locations of record, their hosts and aetiological agents. Ma: macroscopic. Mi: microscopic.

Disease agent(s)	Pathogen(s) species	Pathogen class	Host(s)	Host class	Symptoms	Distribution	Habitat	References
Viral	Phaeovirus	Megaviricetes	<i>Macrocystis pyrifera</i> , <i>Lessonia trabeculata</i> , <i>Ectocarpus</i> spp., <i>Kukuckia</i> sp.	Phaeophyceae	No symptoms detected in LATAM hosts	Chile, Peru, Argentina, Falkland Islands (UK)	Marine	McKeown et al. (2018); this study
Bacterial	<i>Pleurocaspia</i> sp.	Cyanophyceae	<i>Mazzaella laminarioides</i>	Florideophyceae	Ma: dark green spots and gall development	Chile	Marine	Correa et al. (1993, 1997); Buschmann et al. (1997); Faugeron et al. (2000)
	<i>ex Lobocolax deformans</i> (potentially <i>Roseabacter</i> spp. after Ashen & Goff 2000)	Alphaproteobacteria	<i>Neorubra decipiens</i> , <i>Prionitis</i> spp.	Florideophyceae	Ma: warts and galls	Mexico, Peru	Marine	Howe (1914), Dawson (1954), Rodríguez Rodríguez (2018)
	<i>Vibrio owensii</i>	Gammaproteobacteria	<i>Halymenia floresii</i>	Florideophyceae	Ma: Bleaching	Mexico	Marine	Abdul Malik et al. (2022)
Fungal	<i>Chytridium olla</i>	Chytridiomycetes	<i>Oedogonium</i>	Chlorophyceae	Mi: globular extracellular sporangium connected by rhizomycelia to the host cell cytosol	Argentina	Freshwater	Lopez & MacCarthy (1985)
	Undetermined chytrids		<i>Skeletonema</i> , <i>Thalassiosira</i> , <i>Chaetoceros</i>	Mediophyceae		Chile	Marine	Gutierrez et al. (2016)
	<i>Rhizophyidium globosum</i>		<i>Closterium acerosum</i>	Zygnematophyceae		Argentina	Freshwater	Malacalza (1968)
	<i>Rhizophyidium subangulosum</i>		<i>Oscillatoria princeps</i>	Cyanophyceae		Argentina	Freshwater (soil)	Malacalza (1968)
	<i>Phlyctochytrium</i> spp.		<i>Spirogyra</i>	Zygnematophyceae		Cuba	Freshwater	Sparrow (1952a)
	<i>Blyttomyces spinulosus</i>		<i>Spirogyra</i> , <i>Mougeotia</i>	Zygnematophyceae		Cuba	Freshwater	Sparrow (1952a)
	<i>Chytridium lagenaria</i>		<i>Spirogyra</i>	Zygnematophyceae		Cuba	Freshwater	Sparrow (1952a)
	<i>Olpidium entophytum</i>	Olpidiomycetes	<i>Nitella</i>	Charophyceae	Mi: globular extracellular sporangium. Short exit tube	Argentina	Freshwater	Lopez & MacCarthy (1985)
	<i>Ancylistes pfeifferi</i>	Entomophthoromycetes	<i>Closterium</i> sp.	Zygnematophyceae	Mi: intracellular myceliar structure producing external hyphae	Brazil	Freshwater	Berdan (1938)
	<i>Haloguignardia irritans</i>	Sordariomycetes	<i>Stephanocystis dioica</i>	Phaeophyceae	Ma: Galls in basal parts of the host thallus	Mexico	Marine	Aguilar-Rosas (1996)
Fungal-like/ amoeban	<i>Anisolpidium ectocarpii</i>	Peronosporaea	<i>Ectocarpus</i> , <i>Hincksia sandriana</i>	Phaeophyceae	Mi: intracellular spherical syncytium inside host cells, later transforming into a walled spherical to elliptical sporangium. Thin exit tubes of variable length	Chile	Marine	Gachon et al. (2017)
	<i>Eurychasma dicksonii</i>	Peronosporaea	<i>Pylaiella</i> , <i>Ectocarpus</i>	Phaeophyceae	Mi: At early stages, olpidiod intracellular development. At later stages, hypertrophic sporangium with one large or two exit tubes.	Falkland Islands (UK)	Marine	Mystikou et al. (2016)
	<i>Lagenisma coscinodisci</i>	Peronosporaea	<i>Coscinodiscus perforatus</i> var. <i>cellulosus</i>	Coscinodiscophyceae	No symptoms reported for LATAM algal host	Argentina	Marine	Lopez & MacCarthy (1985)
	<i>Myzocyttium proliferum</i>	Peronosporaea	<i>Spirogyra</i> spp.	Zygnematophyceae		Argentina	Freshwater	Lopez & MacCarthy (1985)
	<i>Myzocyttium megastomum</i>	Peronosporaea	<i>Rhizoclonium</i> sp.	Ulvophyceae		Argentina, Cuba	Marine	Pereira & Velez (2004); Sparrow (1952b)

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Table 1 (continued)

Disease agent(s)	Pathogen(s) species	Pathogen class	Host(s)	Host class	Symptoms	Distribution	Habitat	References
	<i>Lagenidium entophytum</i>	Peronosporaea	<i>Spirogyra</i>	Zygnematophyceae		Cuba	Freshwater	Sparrow (1952b)
	<i>Aphanomycoopsis peridiniella</i>	Peronosporaea	<i>Peridiniella</i>	Dinophyceae		Argentina	Marine	Boltovskoy (1984)
	<i>Olpidiopsis porphyrae</i>	Peronosporaea	<i>Porphyra</i> sensu lato, <i>Bangia</i> sensu lato.	Bangiophyceae	Ma: in bladed Bangiales, scattered discolouration alongside the blades. Mi: intracellular spherical syncytium inside host cells, later transforming into a walled sporangium. Exit tubes of variable sizes. In Bangiales, multiple-infected cells have been observed.	Chile	Marine	Murúa et al. (submitted)
	<i>Pythium porphyrae</i>	Peronosporaea	<i>Porphyra</i> sp.	Bangiophyceae	Ma: blade discoloration (from dark red to pink). Mi: intracellular colonization of filamentous mycelia. On heavily infected tissues, mycelia may overgrow the host tissue and form sporangia.	Chile	Marine	Muñoz et al. (2024)
	<i>Maulinia braseltonii</i>	Phytopmyxea	<i>Durvillaea</i> spp.	Phaeophyceae	Ma: Galls -mildly bleached- in stipes and blades. Mi: Hypertrophy in subcortical cells. Development of (unwalled) sporogenic plasmodia. Generation of walled cysts.	Chile, Falkland Islands (UK)	Marine	Aguilera et al. (1988); Goecke et al. (2012); Blake et al. (2017); Murúa et al. (2017); this study
	<i>Maulinia ectocarpii</i>	Phytopmyxea	<i>Ectocarpus</i>	Phaeophyceae	Mi: development of (unwalled) sporangial plasmodia. Generation of free-swimming zoospores. Undigested host cell debris are peripheral, redish to brownish.	Chile	Marine	Maier et al. (2000)
	<i>Woronina glomerata</i>	Phytopmyxea	<i>Vaucheria geminata</i>	Xanthophyceae	Mi: Intracellular development of secondary plasmodia. Cysts are spiky. Undigested host cell debris are peripheral and brownish.	Argentina	Freshwater (soil)	Lopez & MacCarthy (1985)
	<i>Rhizidiomyces apophysatus</i>	Hyphochytridiomycetes	<i>Vaucheria</i>	Xanthophyceae	No symptoms reported for LATAM algal host	Argentina		Marano & Steciow (2006)
	Unidentified rhizopod-like amoeba	Tubulinea	<i>Gracilaria chilensis</i>	Florideophyceae	Ma: Thallus whitening and fragmentation; tissue softening. Mi: perforate the host cell walls of both cortical and medullary cells and digest their protoplasm. Digestion results in large cavities.	Chile	Marine	Correa & Flores (1995)

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Table 1 (continued)

Disease agent(s)	Pathogen(s) species	Pathogen class	Host(s)	Host class	Symptoms	Distribution	Habitat	References
Algal endophytes	<i>Laminariocolax aecidioides</i>	Phaeophyceae	<i>Lessonia</i> spp., <i>Macrocystis pyrifera</i> , <i>Undaria pinnatifida</i>	Phaeophyceae	Ma: dark spots, twisted thalli, bleached irregular galls, pigmented galls, warts. Mi: filamentous brown algae that may reach the medullar interstitial area	Chile, Argentina	Marine	Peters (1991); Thomas et al. (2009); Gauna et al. (2009a); Murúa et al. (2019)
	<i>Laminarionema elsbetiae</i>	Phaeophyceae	<i>Rhodymenia pseudopalmeta</i>	Florideophyceae	Ma: Coverage of brown epiphytes in the host surface. Mi: filamentous brown algae that may reach the medullar interstitial area	Argentina	Marine	Gauna et al. (2009b)
	<i>Microspongium tenuissimum</i>	Phaeophyceae	<i>Glaphyrosiphon intestinalis</i> , <i>Mazaella laminarioides</i> , <i>Sarcothalia crispata</i> , <i>Nothogenia fastigata</i>	Florideophyceae	Ma: Dark spots, irregular warts. Mi: filamentous brown algae that may reach the medullar interstitial area	Chile	Marine	Peters (2003); this study
	<i>Hecatonema</i> sp.	Phaeophyceae	<i>Ulva</i> sp.	Ulvophyceae	Ma: Brown spots on the surface (mostly epiphytic). Mi: May penetrate the host tissue.	Chile	Marine	This study
	<i>Colaconema daviesii</i>	Florideophyceae	<i>Chondracanthus chamissoi</i>	Florideophyceae	Ma: red spots and emerging red filaments on the host surface. Mi: red filaments up to the host medullary section	Chile	Marine	Montoya et al. (2020)
	<i>Colaconema infestans</i>	Florideophyceae	<i>Kappaphycus alvarezii</i>	Florideophyceae	Ma: green patches on host surface and tissue softening. Rarely host deformations. Mi: replacement of host cortical cells by endophyte cells and pathogen filamentous penetration through medullary tissue.	Brazil	Marine	Araújo et al. (2014)
	<i>Ulvella</i> sp.	Ulvophyceae	<i>Mazzaella laminarioides</i>	Florideophyceae	Ma: green spots and patches. Mi: networks of endophytic green filaments across host epidermis and cortex	Chile	Marine	Correa et al. (1994; 1997); Buschmann et al. (1997); Faugeron et al. (2000)
	<i>Epicladia heterotricha</i>	Ulvophyceae	<i>Hymenena falklandica</i>	Florideophyceae	Ma: Patches alongside the thallus. In winter, velvet-like red-brownish patches are formed as filaments emerge for reproduction. Ma: spherical galls on the host. Mi: Colourless parasite forming secondary pit connections with pericentral host cells	Argentina	Marine	Gauna & Parodi (2008)
Algal parasites	<i>Herpodiscus durvillaeae</i>	Phaeophyceae	<i>Durvillaea antarctica</i>	Phaeophyceae	Ma: colourless warts on host branches. Mi: Colourless parasite developed tetrasporangial and gametangial sori, and develop secondary pit	Falkland Islands (UK)	Marine	Fraser & Waters (2012)
	<i>Dawsoniocolax bostrychia</i>	Florideophyceae	<i>Bostrychia</i> spp.	Florideophyceae		Brazil	Marine	Guimarães (1993)
	<i>Spyridiocolax capixabus</i>	Florideophyceae	<i>Spyridia clavata</i>	Florideophyceae		Brazil	Marine	Chen et al. (2019)

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Table 1 (continued)

Disease agent(s)	Pathogen(s) species	Pathogen class	Host(s)	Host class	Symptoms	Distribution	Habitat	References
	<i>Janczewskia moriformis</i>	Florideophyceae	<i>Laurencia</i> spp.	Florideophyceae	connections with its host. Ma: compressed parasite branches emerging from host globular yellowish warts. Mi: endophytic parasite filaments differentiate and establish secondary pit connections with the medullary host cells. Such filaments can overgrow the host tissue disrupting it, and/or develop reproductive structures (game- or tetrasporangia)	Brazil	Marine	Fujii & Guimarães (1999)
	<i>Meridiocolax polysiphoniae</i>	Florideophyceae	<i>Carradoriella denudata</i>	Florideophyceae	Ma: disorganized host growth in apical areas. Mi: parasite cells attached to pericentral cortical host cells.	Brazil	Marine	De Oliveira-Filho & Ugadim (1973)
	<i>Gelidiocolax desikacharyi</i>	Florideophyceae	<i>Gelidium floridanum</i>	Florideophyceae	Ma: Small pustules on the host surface. Mi: parasite cystocarps and tetrasporangia development inside pustules	Venezuela	Marine	Ganesan (1970)
	<i>Gelidiocolax microsphaerica</i>	Florideophyceae	<i>Gelidium pusillum</i>	Florideophyceae	Mi: colourless thallus, interstitially branched. Cystocarps and tetrasporangia may be developed depending on the pathogen life stage.	Mexico	Marine	Dawson (1952)
	<i>Gelidiocolax pustulatus</i>	Florideophyceae	<i>Pterocladia capillacea</i>	Florideophyceae	Ma: Gall-like proliferations in the host, forming adventitious branches. Mi: development of parasite spermatangia inside the host.	Brazil	Marine	Yoneshigue & de Oliveira (1984)
	<i>Gracilariophila</i> sp.	Florideophyceae	<i>Gracilaria</i> sp.	Florideophyceae	Ma: warty or spiky galls in host basal sections, with similar host colouration or bleached areas.	Mexico	Marine	Galicía-García (2017)
	<i>Grateloupiocolax colombianus</i>	Florideophyceae	<i>Grateloupia filicina</i>	Florideophyceae	Ma: Galls on the host branches.	Colombia	Marine	Schnetter et al. (1983)
	<i>Champicolax sarae</i>	Florideophyceae	<i>Champia</i> spp.	Florideophyceae	Ma: Galls on the host branches	Colombia	Marine	Bula-Meyer (1985)
	<i>Spongomorpha aeruginosa</i>	Chlorophyceae	<i>Gigartina fissa</i>	Florideophyceae	Ma: Green spots in the host	Chile	Marine	Hariot (1889)

for DNA extraction and subsequent screening for viral barcodes. These gametophytes have been widely used in mariculture breeding programs [30] and restoration trials [31], and included 57 unisexual strains of *M. pyrifera* (Linnaeus) C. Agardh, *Lessonia spicata* (Suhr) Santelices, *L. berteroa* Montagne and *L. trabeculata* Villouta & Santelices from Chile, Argentina and Falkland Islands (Suppl. Table 2).

2.3. Microscopy

Algal tissues (approximately 1 cm²) were immersed in 8 ml artificial

sterile seawater (ASW; Instant Ocean®) in 6-cm Petri dishes and inspected on an inverted microscope AE2000 (MOTIC™) for pre-diagnosis, prioritizing damaged or diseased areas and diversity of thallus section (e.g. holdfast, stipe, frond). In case of disease suspicion, histological sections (ca. 90 nm) were manually generated from fleshy seaweeds and differential interference contrast (DIC) microscopy was performed either on fresh material or fixed seaweeds in 4 % para-formaldehyde in sterile seawater (PES; [32]). Both DIC and fluorescence images were obtained on a Zeiss Axioscope 5 microscope coupled to an AxioCam 202 mono digital camera, under a Colibri 3 Illumination

System. In case the observations corroborated the presence of endophytic organisms (esp. algal endophytes), sections were put in culture in Petri dishes in Provasoli enriched seawater (PES) for endophyte isolation (see subculturing section below).

2.4. Subculturing of algal endophytes from warts

Endophytes, in contrast to most epiphytes, have demonstrated to have severe impact in the algal host fitness, causing disease [33]. From tissues with confirmed endophytes (after cross section inspection), we followed the protocol described in [34] for isolation. Endophyte raw cultures were initiated from cross sections of diseased areas. The medullar fragments in PES were cultured under white fluorescent light (General Electric, 35 W) at $40 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$, 12 h day^{-1} photoperiod and 12°C , in ASW enriched with PES and supplied the first 2 weeks with $0.1 \text{ mg L}^{-1} \text{ GeO}_2$ [35] and an antibiotic mix (50 mg L^{-1} Penicillin G, 25 mg L^{-1} Streptomycin and 5 mg L^{-1} Chloramphenicol; [36]), to avoid diatom or bacterial contamination. Once filaments emerged from decaying host tissues; apical fragments were excised with surgical blades or Pasteur pipettes with sharp edges and transferred to new dishes with fresh medium to establish clonal isolates. Subcultures were grown under the same conditions. Following this approach, endophytic isolates from *Ulva* sp. Linnaeus, *Nothogenia fastigiata* (Bory) P.G.Parkinson 1983, *Sarcothalia crispata* (Bory) Leister 1993 and *Mazzaella laminarioides* (Bory) Fredericq 1993 were generated (Suppl. Table 1).

2.5. Marker-assisted taxonomy and molecular phylogeny

Endophyte isolates were fixed in either RNeasy® or CTAB buffer as suggested by [37], for DNA extraction. Such samples were directly disrupted manually with individual pestles within 1.5 ml Eppendorf tubes, and incubated in CTAB for 1 h at 65°C . The content was transferred to a new tube, following a phenol-chloroform-isoamyl alcohol (25:24:1) extraction [14]. Alternatively, we used the GeneJet™ DNA extraction kit (ThermoFisher) for back-up samples in case of low yield or poor-quality DNA. Amplifications were performed using the primers pairs GazF2 – GazR2 for brown algal COI mtDNA [34], and MCPf – MCPr for the Major Capsid Protein (MCP) gene amplification (viruses) [38]. Our reactions were performed using an annealing of 55°C for both COI and MCP regions. Amplicons were produced in a total volume of $25 \mu\text{l}$, containing $2 \mu\text{l}$ template DNA, $1 \mu\text{l}$ of each primer at $10 \mu\text{M}$, $9 \mu\text{l}$ PCR water (Sigma-Aldrich) and $12 \mu\text{l}$ REDTaq ready-mix (Sigma-Aldrich). In case of multiple-band products, (common for this MCP PCR reaction), we excised individual bands, which were gel-extracted (GenElute™ gel extraction kit, Sigma-Aldrich), and subjected to a second PCR using the same PCR protocol. PCR products were purified using the High Pure PCR Product Purification Kit (Sigma-Aldrich) and Sanger-sequenced in Macrogen® (Seoul). Resulting chromatograms were checked for quality, and consensus sequences were generated by pair reads were aligned and trimmed using MAFFT [39] with the default settings and a $1\text{PAM/k} = 2$ scoring matrix, coupled in Geneious® v11.0.03 [40]. Consensus sequences (Accessions: PP731879-PP731873 for COI; PP731861-PP731878 for MCP sequences) were primarily blasted for preliminary ID [41] and subjected to phylogeny reconstruction with a representative subset of published brown algal and phaeovirus sequences (obtained after NCBI BLAST searches [42]). Such sequences were aligned using MAFFT, and resulting trees were generated using two different models: RAXML [43] and MrBayes v 3.1.2 [44] as implemented in the Geneious software.

2.6. Atlas construction

Records obtained both by literature review and sampling were plotted in qGIS (QGis.org). Alluvial and chart plots were drafted using R and ggplot [45].

3. Results and discussion

3.1. New records of algal diseases in LATAM

In total, 444 specimens were sampled, equivalent to 25 different species of macroalgae from 6 localities (for details Suppl. Table 1). From these specimens, 12 % looked diseased (presence of galls, warts and/or discolourations) and presented pathogenic organisms. From them 17 were successfully isolated and 14 correctly barcoded.

3.1.1. New records of *Maullinia braseltonii* in *Durvillaea incurvata*

Two pathogens were unable to be barcoded (e.g. low presence, bad DNA quality). In this case, microscopic evidence was used to make a tentative diagnosis. We found *Maullinia braseltonii*, a marine phytomyxid responsible to galls of variable size on the kelp *Durvillaea incurvata* (Fig. 1a). Histological sections of such galls revealed the presence of multiple *Maullinia* secondary plasmodia in hypertrophied subcortical *Durvillaea* cells (Fig. 1b). Samples with these symptoms were found in Estaquilla (41.40°S , 73.84°W), Amortajado Island (41.64°S , 73.67°W) and Mar Brava-Caremapu (41.74°S , 73.74°W ; latter from stranded individuals). These records complement earlier reports for the species in the Southeastern Pacific, broadening the distribution of this parasite across the entire range of its kelp hosts: Southeastern Pacific, Subantarctic islands and New Zealand [14,46,47].

3.1.2. New records of brown algal endophytes

Furthermore, we found algal endophytes associated with disease symptoms (see details in Suppl. Table 3). Dark spots (Fig. 1c) normally occurred superficially (presented as brown crusts) in *Ulva* sp. Nevertheless, on some occasions, filaments emerged from and into these crusts (Fig. 1d), invading *Ulva* interstitium and causing warts and host thallus twisting (not shown). By using a 5'-COI marker, the resulting isolate (UGS5) clustered with good support with *Hecatonema* Sauvageau (Fig. 2), a cosmopolitan epilithic/epiphytic brown alga within the Chordariaceae. *Hecatonema* sp. UGS5 has 95.5 % identity with a *H. maculans* sequence available from GenBank (LM994994), which is a sister species. Moreover, five brown algal endophytes were isolated from three red seaweed species: *N. fastigiata*, *M. laminarioides* and *S. crispata*. These endophytes were found in warts, and were easily recognized in host cross sections, as they are pigmented and allocated in weakly pigmented to unpigmented medullar areas (Fig. 1e). Upon isolation (Fig. 1f) and identification with marker-assisted taxonomy, all the isolated endophytes corresponded to *Microspogium*. Our isolates formed a well-supported clade using the 5'-COI with *M. tenuissimum* isolates already available in Genbank (Fig. 2). Sequence identity among our *M. tenuissimum* sequences and those available in Genbank ranged from 99.1 to 100 %, whereas identities with the sister clade (*M. alariae*) fluctuated between 96.1 and 97 %.

3.1.3. New records of phaeoviruses

From a total of 57 uniclonal kelp gametophytes (Suppl. Table 2), we detected 30 % of them bearing MCP-associated phaeoviral barcodes (Fig. 3). Twelve of these new records corresponded to gametophytes from meridional LATAM (South Patagonia and the Falklands), and three records from northern Chile. One from Bahía Inglesa (also northern Chile) was the only and first record reported associated to the subtropical Pacific kelp *L. trabeculata*, whilst all the rest were detected in *M. pyrifera*. Furthermore, all records from our germplasm belonged to subgroups A and C (sensu [24]). No viral outbreak symptoms were detected during the duration of this work, as described by [38] for the characterization of the genus.

3.2. Historic records of algal diseases in LATAM

Remarkably, we only found 59 published articles related with diseases for LATAM marine flora, spanning only nine countries. In total,

they account for 210 records of algal diseases ranging from viruses (26 records), bacteria (29 records), fungi (28 records), pseudofungi (a.k.a. protists; 39 records), (pathogenic) algal endophytes (41 records) and algal parasites (47 records) (Fig. 4; Suppl. Table 4). Geographically, they distributed majorly within four countries (Chile = 139 records, Argentina = 22 records, Mexico = 21 records and Brazil = 19 records; Fig. 5). We found that Peru, Venezuela and Colombia had very limited records for algal pathogens (<10 records each) although in general, most countries in LATAM have no documentation of those.

3.2.1. Viruses

A breakdown of algal disease agents reported for Latin America is summarized in Table 1. Viruses comprised only asymptomatic dsDNA phaeoviruses (Megaviricetes), detected in wild Laminariales and Ectocarpales from lab isolates and the field [24]. With our survey in regional kelp gametophytes, we incorporated 18 additional records, corroborating a high prevalence within the kelps *M. pyrifera* [38], although we added the first record within *L. trabeculata*. More surprisingly, such records were equivalent to a 30 % of a germplasm used for seaweed

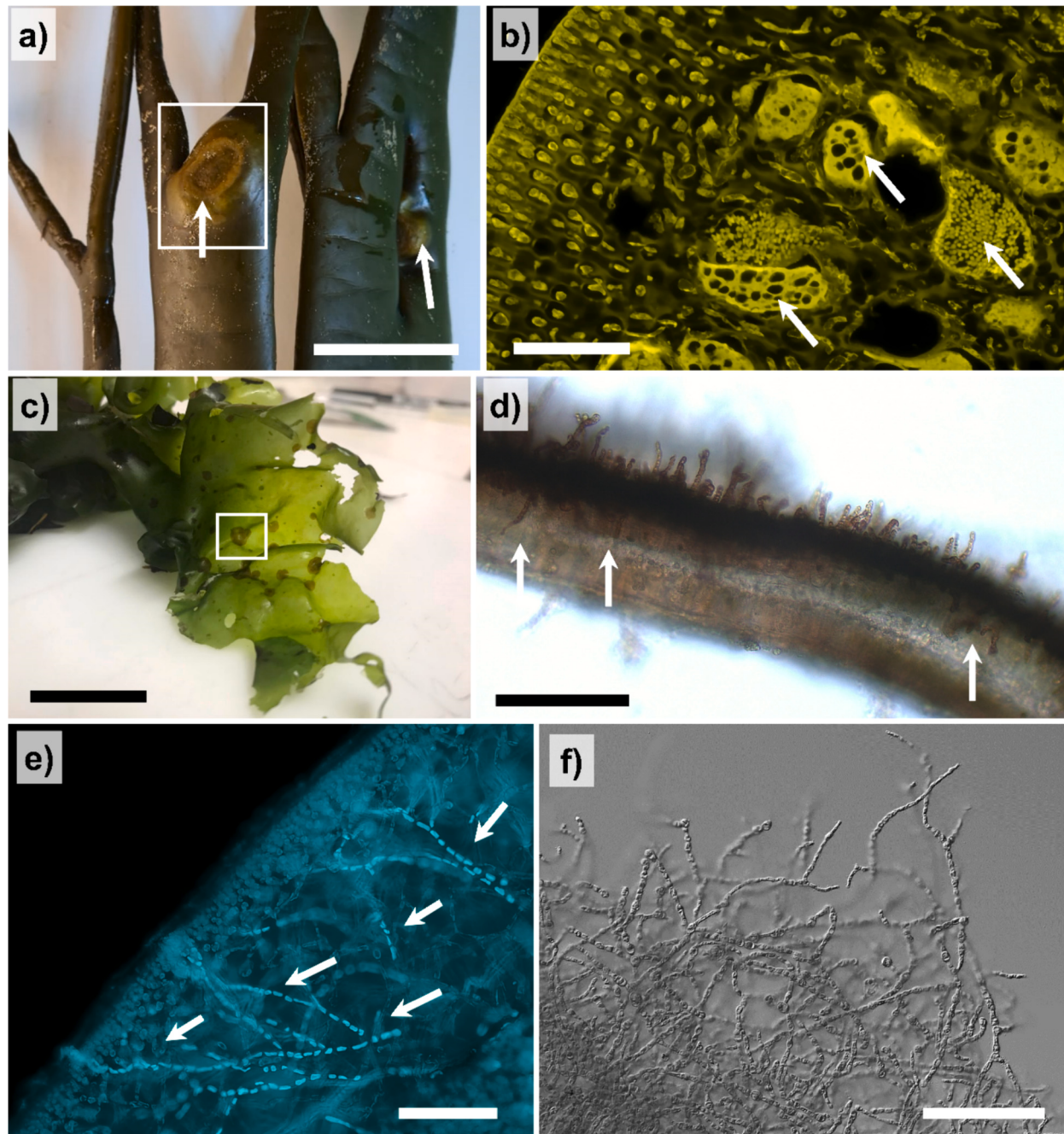


Fig. 1. New records of algal diseases in LATAM, obtained from sampling campaigns during 2020–2022. a) - b) New records of *Maullinia braseltonii* detected in Estaquilla and Amortajado. a) external morphology of galls (arrows). Scale bar: 4 cm. b) cross section of a *Maullinia* gall, showing the early development of sporogenic plasmodia inside hypertrophied *Durvillaea* cells (arrows). Scale bar: 50 μ m. c) - d) Dark spot disease in *Ulva* sp. from Pichi Pelluco, caused by the brown epi-endophyte *Hecatonema* sp. c) external symptomatology. Scale bar: 6 cm. d) endophytic development of *Hecatonema* in its *Ulva* host (arrows). Scale bar: 100 μ m. e) - f) development of brown algal endophytes in scars from red algal hosts. e) endophytic infestation of *Mazaella laminarioides* by *Microsponium tenuissimum*, revealed by chlorophyll autofluorescence. f) clonal isolate of *M. tenuissimum* in culture. Bars in f) and g): 100 μ m. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

mariculture, pointing out a warning signal for future trials of these strains, as the life cycle is not fully understood in these viruses. No virus records were found in both literature review or sampling for red algae or phytoplankton. Red algal viruses are scarcely reported worldwide [48], then this lack of records is not surprising. Nevertheless, phytoplankton viruses are normally well described in terms of viral biodiversity and ecological dynamics [49], which is in great discrepancy to LATAM track records.

3.2.2. Bacteria

Bacterial diseases in the region are also limitedly reported, and majorly reduced to a couple of species. *Pleurocaspia* Thuret is the only endophytic cyanobacterium reported, which causes dark pigmentation and galls in the carrageenophyte *Mazzaella laminarioides* [10]. Ultimately, fitness (e.g. detachment rate, survival) and reproduction (e.g. carpospore germination) were deteriorated after *Pleurocaspia* infection

[50]. Epidemiological studies determined environmental factors are the main trigger for symptom expression, although a potential genetic background may provide additional disease resistance against this pathogenic endophyte [51]. A second bacterial pathogen described for the region was the mislabelled *Lobocolax deformans*, named after an algal parasite in red algae such as *Neorubra decipiens* [52] and *Prionitis* spp. [53]. The disease is characterized by prominent galls or warts that later on were identified as a bacterial dysbiosis [54]. The disease is abundant in tropical waters, although as well as for *Pleurocaspia*, no further records have been reported in the last decades. More recently, *Vibrio owensii* was identified as a pathogen inducing bleaching disease in *Halymenia floresii* grown in an integrated multitrophic aquaculture system [55].

3.2.3. Fungi

Fungal diseases are also poorly documented in LATAM. Free-living

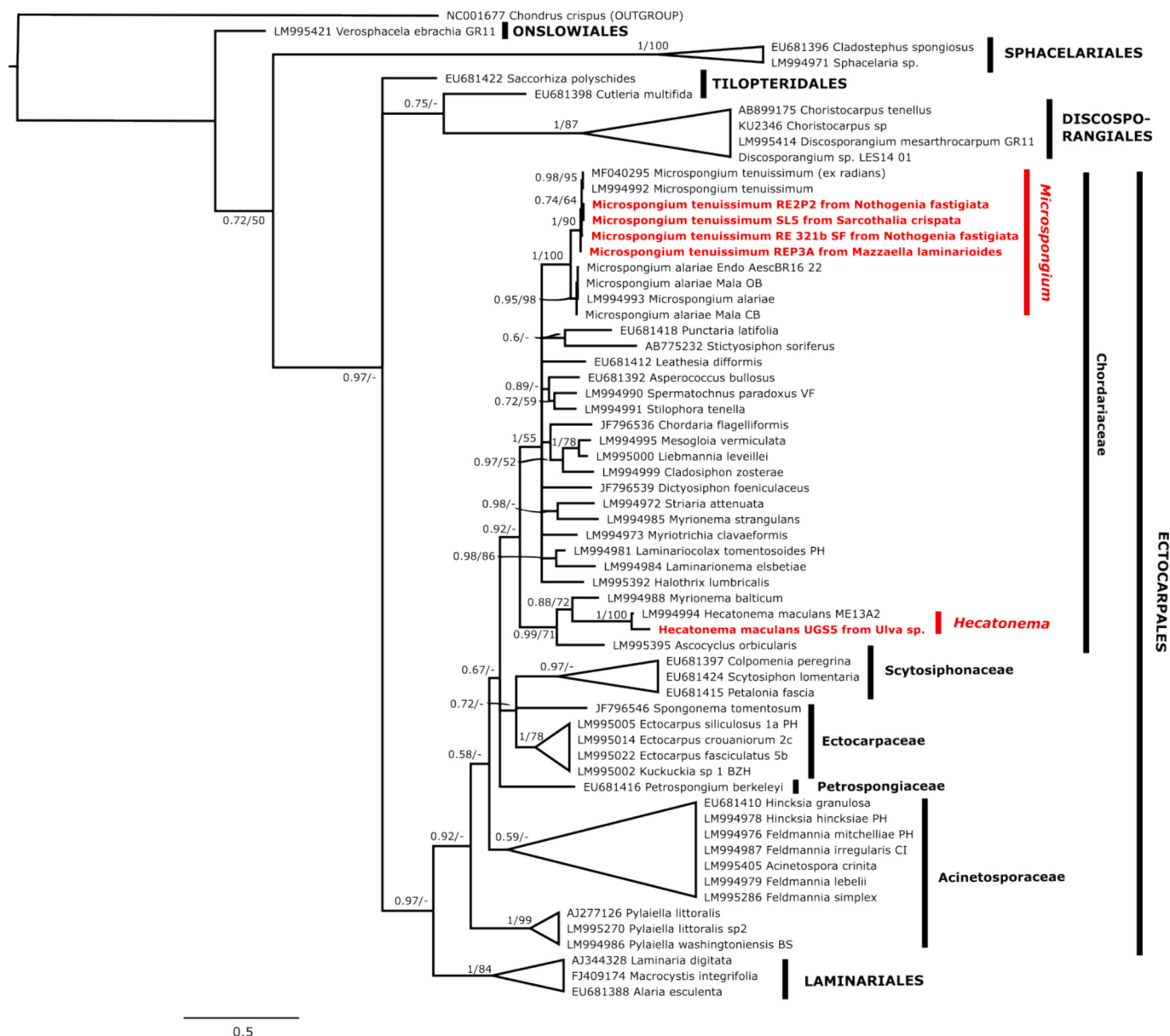


Fig. 2. Molecular phylogeny of brown algal endophytes found in red seaweeds and *Ulva* from southern Chile. MrBayes cladogram of *Microspongium* and *Hecatonema* and representative taxa sequences of Phaeophyceae, based on the 5'-COI nrDNA region. This tree contains a total of 63 sequences and 658 nucleotide positions. Support values correspond to MrBayes posterior probabilities/RAXML bootstrap values. Values lower than 0.5 (or 50 %) were displayed as a hyphen. The scale bar indicates the number of substitutions per site. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

green algae (*Oedogonium*, *Closterium*), cyanobacteria, diatoms (*Skeletonema*, *Thalassiosira*, *Chaetoceros*) and one brown alga (*Stephanocystis*) were reported as targets for fungi from four different classes: Chytridiomycetes [56–58], Entomophthoromycetes [59], Olpidiomyces [60] and Sordariomycetes [61] (Table 1). Most of the studies are taxonomic identification of species of chytrids (*Chytridium*, *Phlyctochytrium*, *Rhizophydium* and *Blyttomyces*), *Ancylistes* and *Olpidium*. One of the most complete studies in terms of distribution is provided by [58] for Chytridiomycota abundance in the Humboldt current system off Chile, which were associated with *Thalassiosira* and *Chaetoceros* abundances in

a host-specific manner, but particularly high in austral spring. This study also helps to provide additional evidence from the big South about the role of parasitism in microbial dynamic in aquatic communities, including organic carbon transfer alongside trophic levels. Another fungus associated with disease macroalga was *Haloguignardia irritans*, an Ascomycota tumorigenic on *Stephanocystis dioica*. The pathogen is abundant off Californian coasts, causing malformation in stipes and basal fronds of its host.

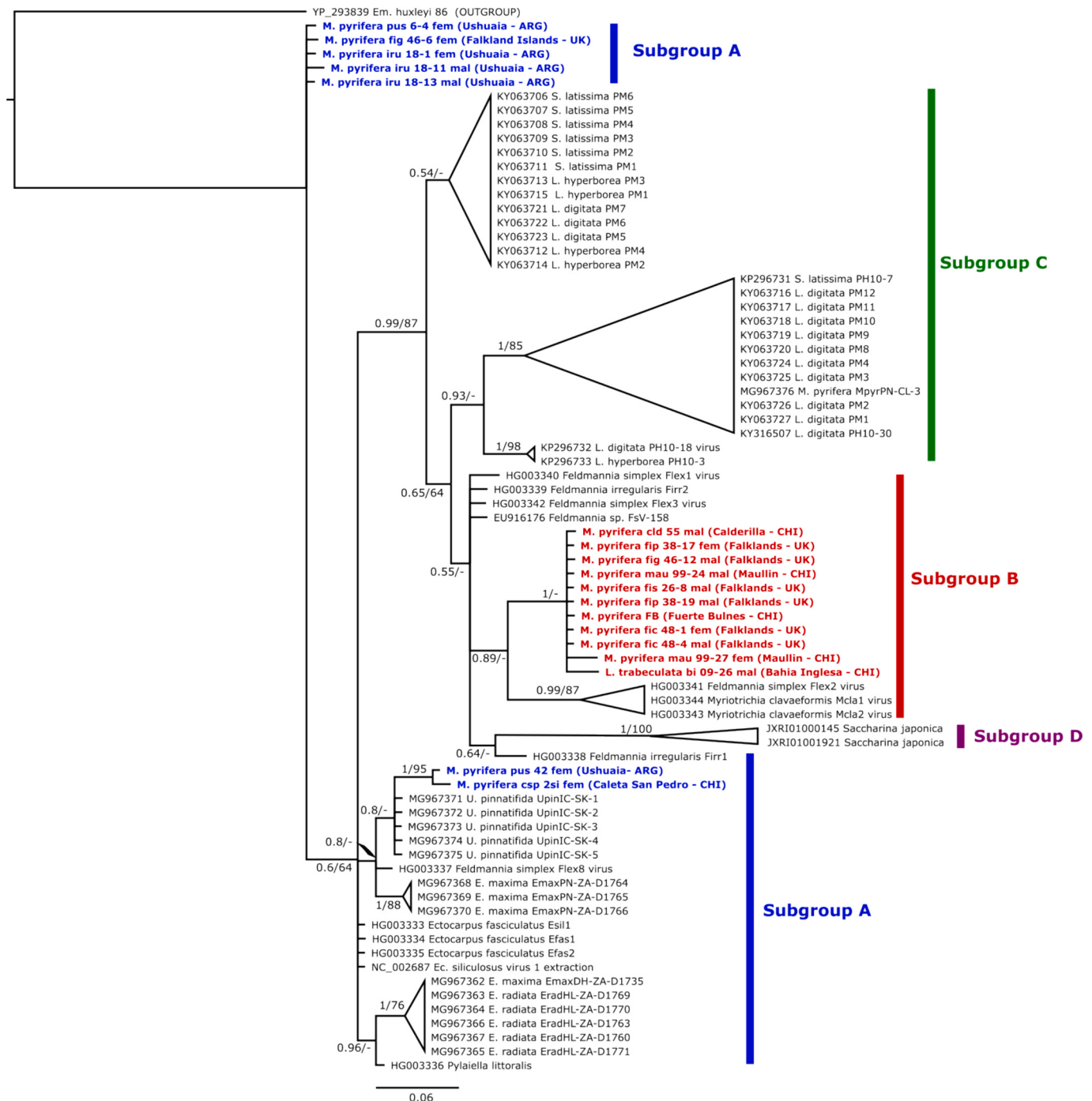


Fig. 3. Molecular phylogeny of phaeoviruses found in kelp gametophytes from southern Chile. MrBayes cladogram includes Chilean kelp gametophytes (MCP positives) and representative taxa sequences of phaeoviruses, based on the MCP region. This tree contains a total of 76 sequences and 85 amino acid positions. Support values correspond to MrBayes posterior probabilities/RAxML bootstrap values. Values lower than 0.5 (or 50 %) were displayed as a hyphen. The scale bar indicates the number of substitutions per site.

3.2.4. Protistan pseudofungi

A larger biodiversity of algal diseases was reported associated to fungal-like (a.k.a. pseudofungal or protist) pathogens. Some correspond to single records of Tubulinea affecting *Gracilaria chilensis* [11] and Hyphochytridiomycetes (*Rhizidiomyces apophysatus*) that infect *Vaucheria* [62]. Oomycota, on the other hand, represent a plethora of pathogens infecting brown, red, green, diatom and dinoflagellate hosts. Microalgal-associated oomycetes belonged to *Myzocyttium*, *Lagenisma* and *Aphanomycopsis* genera, found in freshwater green algae, diatoms and dinoflagellates [60,63]. Additionally, one record of *Myzocyttium megastomum* infecting the green filamentous alga *Rhizoclonium* [64], corresponded to the only finding linked to Ulvophyceae seaweeds from LATAM. *Eurychasma dicksonii* and *Anisoplidium ectocarpii* are two early diverging oomycetes parasitic of brown algae, detected in both south-eastern Pacific and southwestern Atlantic [65,66]. After transfection into stable pathosystems, laboratory studies have demonstrated a wider range of hosts from up to eight different phaeophyceae orders, including sporophyte and gametophyte stages of Laminariales (e.g. *Macrocystis pyrifera*) [67,68]. The generation of such pathosystems (incl. Latin American strains) has allowed a better understanding of disease susceptibility in brown algae [37], including the studies of novel disease resistance mechanisms such as oxidative stress [69], cell wall reinforcement [70], and the inducibility of a suicidal pathogen's autophagy [71]. *Olpidiopsis porphyrae*, another obligate intracellular oomycete and symbiont on red algae, was recently described in southern Chile, associated with *Bangia*, *Porphyra* and *Pyropia* spp. (Murua et al. submitted). This species is the aetiological agent for the *Olpidiopsis* blight disease, one of the main disease risks in laver aquaculture in Asia. In LATAM, the disease is abundant during autumn and winter. *Pythium porphyrae*, the aetiological agent for the red rod disease also in bladed Bangiales, has also been recorded in Chile, but in this case as a natural biocontrol agent of *Porphyra* sp. pest outbreaks on farmed *Gracilaria* [72]. Both diseases affect commercial laver species normally traded in local markets and

incipiently cultivated in Chile.

As relevant as oomycetes, phytomyxids (a.k.a. Plasmodiophorids) are pervasive pathogens infecting algae. In LATAM, punctual cases have been recorded for *Woronina glomerata* infecting *Vaucheria* in lake systems in Argentina [60] and *Maullinia ectocarpii* parasiting an *Ectocarpus* sp. from an estuary in southern Chile [73], but also associated with *Durvillaea* galls [47] (Table 1). *M. ectocarpii* I. Maier, E. R. Parodi, R. Westermeier et D. G. Müller is currently the only seaweed-associated phytomyxid (order Phagomyxida) transfected and maintained as a reproducible pathosystem inside brown algal hosts, whereby it is being used to understand host ranges, virulence, growth dynamics and nutrition aspects of these cryptic organisms [74,75]. A sister species, *M. braseltonii* P. Murúa, F. Goecke et S. Neuhauser, is one of the most significant phytomyxids in LATAM coasts. It is widespread in subantarctic coasts alongside its host (*Durvillaea*), causing the *Maullinia* gall disease [14,76]. *Durvillaea* spp. are a valuable seaweed resource in Chile [77]. How this disease interacts with bull kelp fisheries and affects *Durvillaea* populations is virtually unknown in the region.

3.2.5. Algal endophytes

Other groups of pathogenic organisms associated with seaweeds are algal endophytes, whereby parasitism (by means of nutrient translocation) is not demonstrated, yet in certain conditions can cause disease symptoms. Rhodophyceae seaweeds are one the most affected by endophytism (Table 1). Particularly in LATAM, red seaweeds have been described with pathogenic interactions with filamentous brown (*Microspongium* [33], *Laminarionema* [78]), red (*Colaconema* [79,80]) and green algae (*Ulvella* [50,51,81,82], *Epicladia* [83]) (Table 1). Brown (kelps) and green algae (*Ulva* sp.) also have records for *Laminariocolax* [84–86] and *Hecatonema* genera (this study), respectively. Symptoms for endophytes varied from dark patches and entwisting blades to gall emergences and malformations. In several cases such endophytes do not cause visible symptoms. Nevertheless, ultimately, they may lead to the

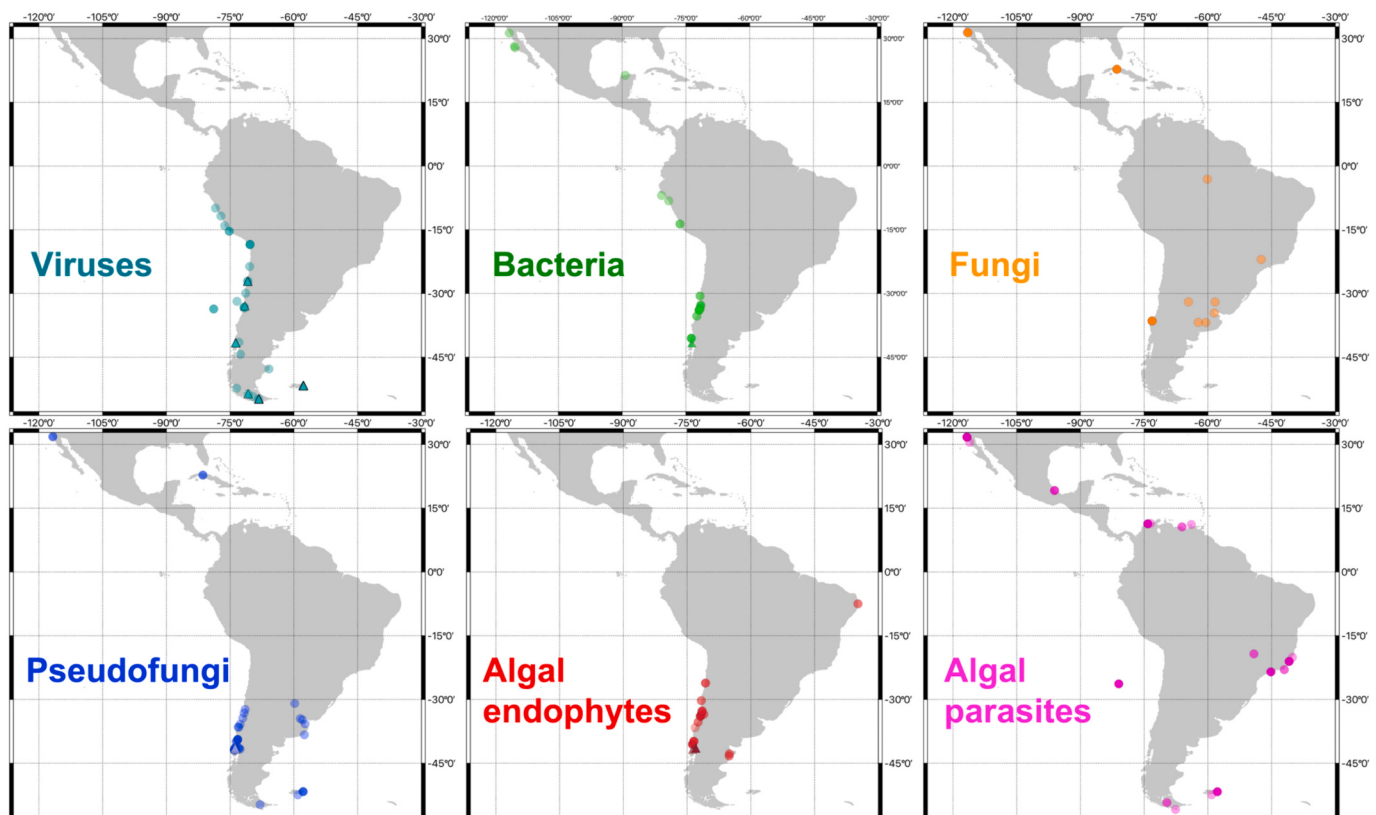


Fig. 4. Geographic distribution of historic (circles) and present (this study, triangles) algal disease records in LATAM, for six representative algal pathogens.

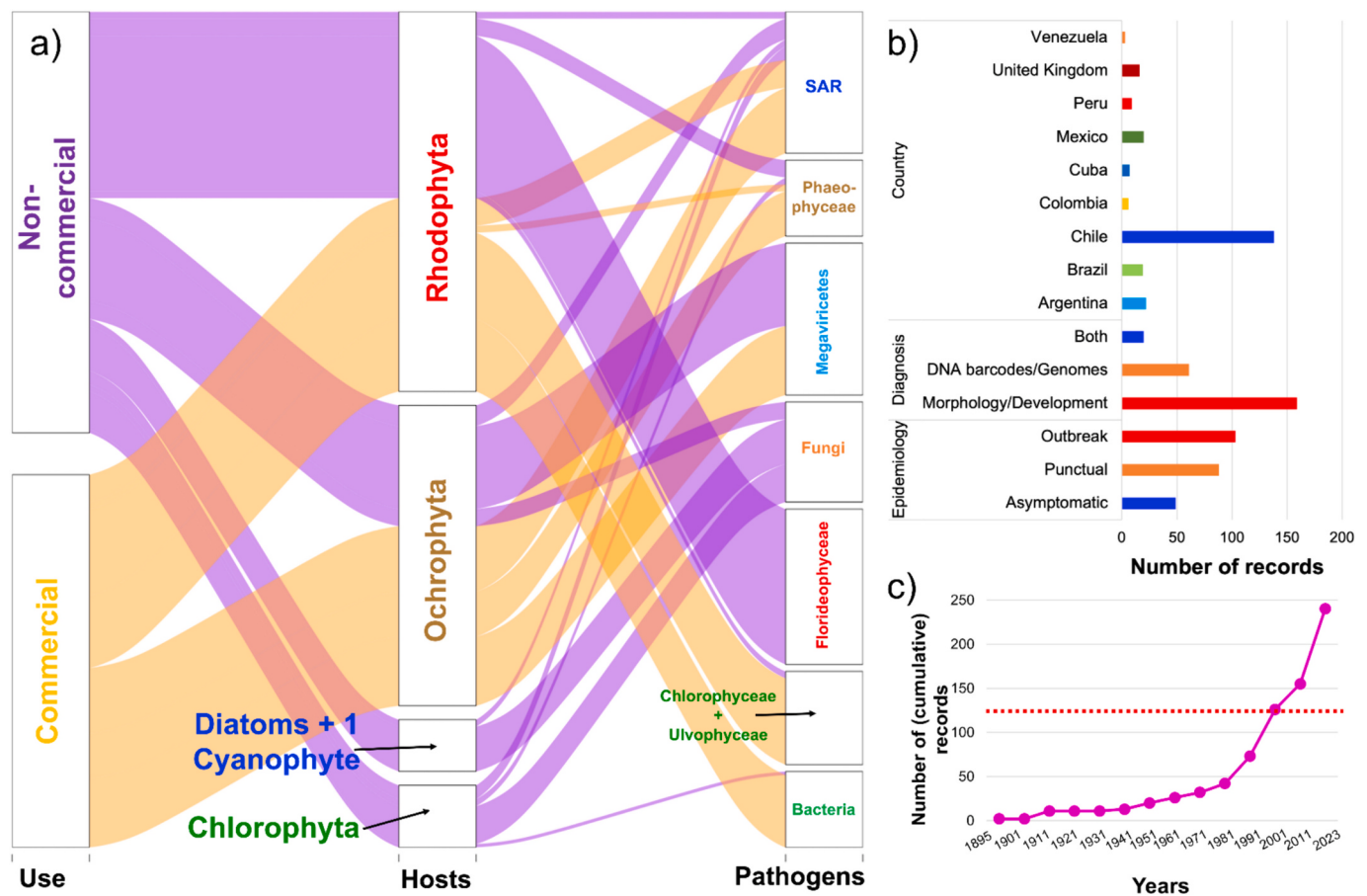


Fig. 5. Features of historic LATAM algal disease records. a) Alluvial plot representing the 242 records of LATAM algal pathogens, aggregated by host use (Commercial – non-commercial), host and pathogen taxonomy. Bacteria include both endophytic (yet pathogenic) and parasitic bacteria, and SAR does not include photosynthetic organisms. b) distribution of records by country, diagnosis type and epidemiology. c) evolution of reported algal disease records for LATAM since 1895. Red line indicates half of the historic regional records. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

breakdown and detachment of fronds. Most of the studies show these endophytes as punctual findings, which means they are rarely showing visible symptoms in nature. In the Chilean kelp *Lessonia berteroana*, nevertheless, it seems endophytism by *Laminariocolax acidioides* is quite pervasive, reaching 100 % of the populations at some point of the year [9]. In such context it is unclear the extent of resistant strains that already are available in the wild, but more importantly, it is unknown how human or environmentally these outbreaks are mediated in nature.

3.2.6. Algal parasites

True algal parasites have also been described for the region (Table 1). Except for the brown alga *Herpodiscus durvillaeae* from Falkland Islands [87] and *Spongomorpha aeruginosa* (ex *Chlorochytrium inclusum*) [88], all parasites described are red algal parasites (Ceramiales and Rhodymeniales). They are characterized by diminished morphologies, with reduced photosynthetic activities, causing colourless warts and galls in their hosts (Table 1). Similarly as worldwide algal parasites, they are phylogenetically related to their hosts [89], with the exception of *S. aeruginosa*, parasitic on *Gigartina fissa* (Suhr) J.Agardh. Records in LATAM are punctual, and most of them are tropical seaweeds from Brazil [90–95], Mexico [96,97], Colombia [98,99] and Venezuela [100,101], and few records from Chile and Falkland Islands [102]. Epidemiological data is overall limited for the region.

3.3. General picture from LATAM algal disease records

Our literature review of algal disease records in LATAM showed

several biases. For instance, 50 % of the records have been obtained in the last 20 years. Furthermore, most of the hosts detected in LATAM records belong to red or brown algae (Fig. 5). Within those, a significant percentage (53 %) are considered economically-relevant algae (e.g. used in human activities such as food, feed or commodity), which in total account for 16 species. Nevertheless, only a small fraction (14 %) comes from farming set-ups. Ca. 40 % of these records were obtained from algal populations showing outbreaks for the associated disease, whereas 50 % were named as punctual findings, where a limited number of hosts (one or few algae) showed disease symptoms. Few of them were asymptomatic, yet traces of diseases have been detected at molecular level (e.g. lysogenic phaeoviruses in brown algae). Another bias is spatial, whereby only 9 (out of 33) countries have records, and Chile bears 66 % of the current records for algal diseases for the whole region, in contrast to more than ten countries with no traceable record available. Additionally, there is a diagnosis bias, whereby <10 % complement both molecular and morphological techniques to generate disease diagnoses.

4. Conclusion

In the present study, we compiled the pathogens associated with LATAM algae, which may be threat for ongoing farmed seaweeds (e.g. agarophytes or carrageenophytes), but alternatively may also act as substantial regulators of wild stocks. Regional records were biased by country, host-pathogen system detected, diagnoses and intensity of disease, associated with very contrasting sampling efforts toward seaweed flora and/or algal diseases. Moreover, LATAM records seem

rather insufficient to capture the actual pathogen biodiversity for the region, in comparison to other latitudes (e.g., Asia, [8]). For example, by adding our new records to this historical list, we expanded the LATAM algal disease baseline by 15 %, only with few non-extensive sampling campaigns, suggesting a significant increase of these records in the upcoming years. This monitoring should be a collaborative effort, not only at regional level but also transversal to all the institutions affected (i.e. from farmers to policymakers), in order to keep diagnoses updated in real time with the increasing new records [103].

In the light of the evidence presented here, diseases may pose a similar menace for LATAM future seaweed aquaculture, as roughly 50 % of pathogens listed here were reported for algae with economic relevance. Therefore, their elucidation seems fundamental to ensure a sustainable development of the industry. Tools to aid this elucidation should be strengthened by local actors [103], and applied in a more active way in order to anticipate biosecurity problems like in Asian or African regions [23], whereby seaweed aquaculture is well established but struggling with emerging diseases. We are at such an incipient stage in terms of aquaculture in LATAM that impacts associated with disease dissemination may be alleviated before they affect the industry and the environment [28], and for that aim rising complete baselines are mandatory in order to adapt national- and regional-wide frameworks [7].

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.algal.2024.103604>.

Statement of informed consent, human/animal rights

No conflicts, informed consent, human or animal rights applicable.

Declaration of authors' agreement

All authors agreed to the authorship and submission of the manuscript to Algal research for peer review.

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CRedit authorship contribution statement

Pedro Murúa: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Liliana Muñoz:** Writing – review & editing, Methodology, Investigation, Formal analysis, Data curation. **Danielo Bustamante:** Writing – review & editing, Methodology, Investigation. **Cecilia Gauna:** Writing – review & editing, Methodology, Investigation. **Leila Hayashi:** Writing – review & editing, Methodology, Investigation. **Daniel Robledo:** Writing – review & editing, Methodology, Investigation. **Martina Strittmatter:** Writing – review & editing, Methodology, Investigation, Conceptualization. **Paola Arce:** Writing – review & editing, Methodology, Investigation, Conceptualization. **Renato Westermeier:** Writing – review & editing, Methodology, Investigation. **Dieter G. Müller:** Writing – review & editing, Methodology, Investigation. **Claire M.M. Gachon:** Writing – review & editing, Methodology, Investigation, Formal analysis, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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