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ARTICLE

Similarity and areas of endemism of the *Laurencia* complex (Ceramiales, Rhodomelaceae) in Cuba

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Resumen

Similitud y áreas de endemismo del complejo Laurencia *(Ceramiales, Rhodomelaceae) en Cuba*

Las especies del complejo *Laurencia* son elementos importantes en la estructura y diversidad de los ecosistemas costeros. Por primera vez, se analiza la distribución geográfica del complejo dentro de la plataforma cubana, sus áreas marinas protegidas y se identifican áreas potenciales endémicas, considerando las ecozonas en que se dividió la plataforma. A la fecha, se han inventariado 19 especies, de estas 10 pertenecen a *Laurencia*, una a *Osmundea*, cinco a *Palisada*, dos a *Yuzurua*, y se incorporó *Laurenciella* como nuevo género para Cuba. La distribución fue desigual, con un alto número de especies y puntos de ocurrencia, especialmente en las regiones Occidental y Central de la costa norte. El análisis de parsimonia de endemicidad indicó dos ecozonas, una en Habana-Matanzas y otra en la Costa Nordeste, sustentadas por tres y dos especies endémicas, respectivamente.

Palabras clave: Biogeografía marina; Conservación; Análisis de parsimonia de endemicidad; Algas rojas

Abstract

Species of the *Laurencia* complex are important elements in the structure and diversity of coastal ecosystems. For the first time, we analyzed the geographical distribution of the complex within the Cuban shelf, its marine protected areas and identified potential endemic areas, considering the ecozones into which the shelf was divided. To date, 19 species have been inventoried, of which 10 belong to *Laurencia*, one to *Osmundea*, five to *Palisada*, two to *Yuzurua*, and *Laurenciella* a new record of genus for Cuba. The distribution was uneven, with a high number of species and occurrence points, especially in the Western and Central regions of the northern coast. The parsimony analysis of endemicity indicated two ecozones, one in Habana-Matanzas and the other in the Northeast Coast, supported by three and two endemic species, respectively.

Key words: Marine biogeography; Conservation; Parsimony analysis of endemicity; Red seaweeds.

Introduction

Cuba is the largest archipelago in the Caribbean Sea. It includes the main island of Cuba, Isla de la Juventud, and about 4000 islands and keys, which host the highest marine biodiversity in the region (Miloslavich *et al.* 2010, Roman 2018). The Cuban archipelago is surrounded by the deep basins and trenches of the Caribbean Sea, the Gulf of Mexico, the Straits of Florida, and the Bahamas. Extensive reefs border the shelf for most of its length before steeply descending to a depth of 400 m or more (Claro 2006, García-Machado *et al.* 2018). This configuration promotes divergent ecosystems that support many species throughout their different life stages. Among the main biotopes present on the Cuban shelf are non-reef rocky bottoms, coral reefs, seagrass meadows, estuaries, beaches, mangroves, and rocky intertidal zones (García-Machado *et al.* 2018).

The patterns of species composition and richness of the algal assemblages in the Cuban archipelago result mainly from the coastal proximity of the islands and archipelagos that make up the Caribbean, the southern Gulf of Mexico, and Florida (Suárez & Martínez-Daranas 2020), combined with large and mesoscale oceanographic patterns (Claro 2006, Suárez *et al.* 2015).

The marine algal flora of Cuba has been extensively studied over the past centuries, receiving more attention in the last decades in the areas of systematics and ecology (Montagne 1842, Farlow 1871, Howe 1917, Suárez *et al.* 2015). However, phytogeographic studies are still scarce (Suárez 1984, 1989a, Suárez *et al.* 2008, Suárez & Martínez-Daranas 2020), and are lacking particularly for the algae of the *Laurencia* complex.

Within the order Ceramiales (Rhodophyta), the *Laurencia* complex is the best represented, with 396 species of red macroalgae. However, currently, only 213 are accepted taxonomically (Guiry & Guiry 2022), which are distributed in the genera *Laurencia* J.V. Lamouroux *sensu stricto* (*s.s.*), *Osmundea* Stackhouse, *Chondrophycus* (Tokida & Y. Saito) Garbary & J.T. Harper, *Palisada* K.W. Nam, *Yuzurua* (K.W. Nam) Martin-Lescanne, *Laurenciella* Cassano, Gil-Rodríguez, Sentíes, Díaz-Larrea, M.C. Oliveira and M.T. Fujii, *Corynecladia* J. Agardh, and *Ohelopapa* F. Rousseau, Martin-Lescanne, Payri, and L. Le Gall.

For the Caribbean and the Gulf of Mexico, 41 species and two varieties are currently recognized, distributed in seven genera within the complex. The genus *Corynecladia* has not yet been recorded for this region. To date, *Laurencia*, *Osmundea*, *Palisada* and *Yuzurua* have been reported in Cuba based on morphological and molecular data (Cassano *et al.* 2012, Sentíes *et al.* 2015, Suárez *et al.* 2015, Fujii *et al.* 2016). Recently, González-Sánchez *et al.* (unpublished) also found the genus *Laurenciella* in Cuba. A list of records of the *Laurencia* complex for the Cuban archipelago is presented in Supplementary Material 1, Table S1).

Cuba shows the highest richness within the large islands of the Caribbean region, with 19 species and two varieties. All members of the *Laurencia* complex found along the Cuban coasts have also been reported in the Atlantic coasts of Central America, Florida, Bermuda and the Gulf of Mexico, except for *Palisada furcata*, which was recorded only in Brazil. However, these values are still low since they represent less than 50% of the taxa reported for this region.

At present, knowing the species richness and distribution patterns in an area is a priority for science, especially when the ecosystem functions decline due to increased anthropogenic threats and climate change (Hall *et al.* 2013). Estimating species richness and distribution changes would provide critical ecological perspectives for conservation and understanding of how they react to environmental perturbations (Primack *et al.* 2018). Furthermore, estimating the areas of endemism for a particular taxon using tools such as the parsimony analysis of endemism (PAE; Morrone 2014), is useful to identify priority areas for conservation (Posadas & Miranda-Esquivel 1999).

Suárez *et al.* (2015) mentioned the areas of the Cuban shelf where species of the *Laurencia* complex have been recorded. However, the richness of these algae and their distribution patterns in shelf areas remain to be characterized. This work aimed to describe the distribution patterns of the species composition of the *Laurencia* complex in Cuba.

Materials and methods

Sampling sites

Samples were collected between 2017 and 2019 in the intertidal or subtidal zone (0-2 m) at 21 sites of the Cuban archipelago, representing the nine

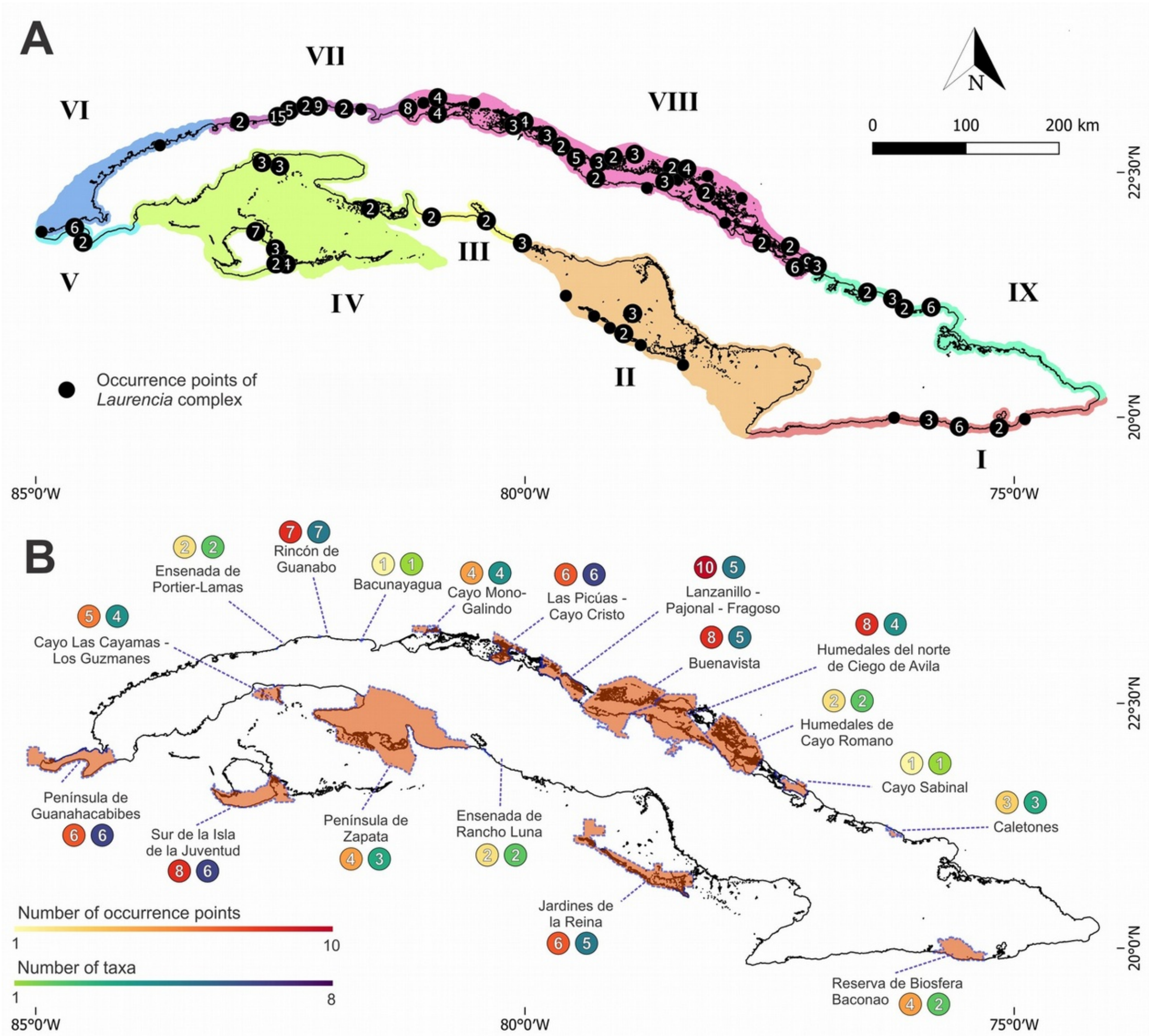

Figura 1. Distribución del complejo *Laurencia* dentro del archipiélago cubano. **A:** Puntos de ocurrencia recogidos por las zonas ecológicas propuestas por Areces (2002). Cuando se registró más de un punto de ocurrencia en la misma localidad, el número total de puntos se muestra en puntos negros. **B:** Áreas marinas protegidas (AMP: polígonos rojos) con registros del complejo *Laurencia*. Los números correspondientes de puntos de ocurrencia (izquierda) y taxones (derecha) registrados dentro de cada área se muestran junto a sus nombres.

Figure 1. Distribution of the *Laurencia* complex within the Cuban archipelago. **A:** Occurrence points gathered by the ecological zones proposed by Areces (2002). When more than a single occurrence point was recorded in the same locality, the total number of points is shown in black dots. **B:** Marine protected areas (MPAs: red polygons) with records of the *Laurencia* complex. The corresponding numbers of occurrence points (left) and taxa (right) recorded within each area are shown next to their names.

ecological zones (ecozones hereafter) established during a 2001 workshop (Areces 2002, Fig. 1A).

Morphological observations and data collection

For molecular analysis, small thallus fragments from each sample were dried on silica gel. The remaining material was preserved in 4% formalin-seawater or as herbarium vouchers for morphological studies. Transverse and longitudinal hand sections were obtained with a razor blade, stained with 0.5% aqueous aniline blue, and acidified with 1N HCl (Tsuda & Abbott 1985). Habitat images and photomicrographs were taken using a Panasonic Lumix DMC-FH4 camera (Panasonic Corporation, Osaka, Japan) coupled to a Zeiss Stemi 2000-C stereomicroscope and a Zeiss Primo Star microscope (Carl Zeiss Microscopy, Göttingen, Germany).

Voucher specimens were deposited in the herbarium of the Botanical Institute, São Paulo (SP), and in the National Aquarium of Cuba collections. Additionally, we examined specimens of the *Laurencia* complex deposited in the following herbaria: a closed collection of “Instituto de Oceanología” (IDO); the herbarium of “Acuario

Nacional de Cuba" (HANC); Universidad Autónoma Metropolitana-Iztapalapa (Metropolitan Herbarium-UAMIZ); the herbarium of "Instituto de Botanica de São Paulo" (SP); the University of Michigan Herbarium (MICH); the US National Herbarium, Department of Botany, Smithsonian Institution (NMNH); the New York Botanical Garden Herbarium (NY); Bernice Pauahi Bishop Museum (BPBM; current code: BISH); and the Museum National d'Histoire Naturelle (MNHN). Herbarium abbreviations follow the online Index Herbariorum (http://sciweb.nybg.org/science2/IndexHerbariorum.asp) (Thiers 2021, continuously updated).

Infrageneric taxa of the *Laurencia* complex for Cuba from the online database AlgaeBase (Guiry & Guiry 2022) were used as complementary data. Distribution maps were prepared using Quantum-GIS 3.10 software, considering the nine ecozones (Fig. 1A).

Ecozone delimitation within the Cuban insular shelf was made from an *a priori* definition according to the observation scale. However, some biogeographic aspects were considered, such as the habitat geographic "place" or "location" in the coastal zoning of the Cuban insular shelf and its nature. The habitat nature was derived from the substrate type and degree of bottom coverage (Areces 2002, Areces & Salinas-Chávez 2020).

Characteristics of the nine ecozones (Fig. 1A)

I-Southeast: this coastline is high and steep, with a predominance of rocky substrates and a very narrow shelf. It has no keys or low areas, and the beaches are made of pebbles.

II-South Central (Jardines de la Reina): includes Guacanayabo and Ana María gulfs, and the Jardines de la Reina archipelago. Mangroves, coastal lagoons, muddy and sandy-muddy bottoms predominate in the gulfs, where the coral patches are commonly known as "heads". Keys and reef lagoons have well-developed seagrass meadows. The archipelago is to the South, bordering the gulfs, and has a great development of coral reefs.

III-South of the Guamuhaya Massif: is one of the smallest areas (Fig. 1A). It has a narrow shelf, with a rocky coast and estuarine characteristics in Cienfuegos Bay, such as muddy and sandy-muddy bottoms and mangroves. These estuarine characteristics are the result of the contribution of the rivers and the low tidal energy; it receives the drainage of urban and industrial waste from the city.

IV-Batabanó-Canarreos: it includes the Gulf of Batabanó and the Canarreos Archipelago. This area is dominated by seagrasses, with some rocky areas to the southwest, and coral reefs bordering the outer shelf edge.

V-Southwest of Guanahacabibes: it is an abrasive karst coastline, with some sandy beaches and a narrow shelf in its entirety, 200 to 300 m wide. Rocky substrates, coral reefs, and sandy bottoms predominate in this area.

VI-Northwest (Los Colorados): this archipelago includes keys and banks with well-developed coral reefs. The interior has muddy and sandy-muddy bottoms, with a great development of seagrasses and coastal mangroves, and some beaches.

VII-Habana-Matanzas: it is an area without keys. It has a narrow shelf, with sections of cliffs, important bays with mangrove, coastal reefs dominated by rocky ledges, rocky intertidal, and sandy beaches with seagrasses in some reef lagoons. Most research has been directed to studying coral reefs, the most abundant ecosystems in this area. The largest territory is part of the highly anthropized coastal area of Havana, the capital of the country.

VIII-North Central (Sabana-Camagüey): it is an extensive area with a wide shelf, keys, and islets; between these and the main island´s coast are extensive water bodies with soft bottoms and seagrasses. North of the keys, the area is bordered by coral reefs with reef lagoons.

IX-Northeast: as in the Southeast, the shelf is narrow but has several important bays and all kinds of substrates and biotopes, including coral reefs and rocky intertidal zones.

Currently, Cuba has 211 conservation areas for protection, including 105 Marine Protected Areas (MPAs) (CNAP 2013, Perera Valderrama *et al.* 2018). Fifty-seven of the proposed areas have been approved, and seven are currently in approval. Approved MPAs protect more than 2.5 million hectares of marine and coastal territories in the 15 provinces of Cuba and the special municipality of Isla de la Juventud. Individual MPAs and their locations are available at http://www.snap.cu/index.php/ct-menu-item-15.

Marine protected areas are considered of international, national, or regional importance. They constitute the core of the National System of Protected Areas (SNAP) due to their conservation value, representativeness, degree of conservation, uniqueness, and size (Perera Valderrama *et al.* 2018). Cuban MPAs are also classified according to national (n=46) and local (n=59) significance. These protected areas occupy a large part of the marine-coastal territory of the archipelago. For this reason, we consider it important to include the distribution of the species of the *Laurencia* complex recorded within the Cuban MPAs in our analysis (Fig. 1B, Table 1).

Analysis of data

The species composition of the *Laurencia* complex was compared between ecozones using Sørensen´s similarity index (Sørensen 1948). This index relates the number of species in common with the arithmetic mean of the species in the sites where they coincide (Magurran 1988). A clustering analysis (CLUSTER) was performed with this matrix, using the linkage method by group average (UPGMA) and 10,000 replacements. According to the highest percentage of replacement supported by each node within the cluster, a cut off line was established in the dendrogram (Hammer *et al.* 2001).

ANOSIM analyses were also employed to test for differences between similarity groups, following the criterion of the cut off line and using 10 000 permutations and Sørensen´s similarity index (Clarke & Warwick 2001). Similarity percentage (SIMPER) analysis was used to calculate the contribution of the species that most influenced the dissimilarity between groups (Clarke 1993).

Additionally, a distance-based test for homogeneity of multivariate dispersion (PERMDISP, Anderson 2006) and a non-metric multidimensional scaling (nMDS) analysis (Clarke & Warwick 2001) were performed to interpret and visualize data patterns. These analyses were based on 10 000 permutations and Sørensen´s similarity index (Clarke & Gorley 2006). All statistical analyses were performed with Past 4.07b (Hammer *et al.* 2001).

To identify endemism hotspots for the *Laurencia* species complex, we ran a parsimony analysis of endemicity (PAE) (Morrone 1994, 2014) using Nona 2.0 (Goloboff 1999) and Winclada v. 1.00.08 as a graphic interface (Nixon 2000). PAE uses a grid cell species matrix to identify endemism hotspots for a group. We adopted a 1.5° grid size for the analysis, with all cells encoded with an alphanumeric pattern. A presence/absence matrix was constructed, including a hypothetical taxon absent in all cells to root the resulting tree (Morrone 1994, 2014, Morrone & Crisci 1995, Posadas & Miranda-Esquivel 1999). For this analysis, 100 replicates were performed using TBR ("tree bisection and reconnection") as the adopted heuristic search algorithm and retaining a maximum of 1000 trees in each replicate. Most parsimonious trees were used to produce a strict consensus tree. On this tree, endemic areas were identified when at least two exclusive species supported them (Morrone 1994).

Results

Nineteen species of the *Laurencia* complex were recorded for the Cuban archipelago (Supplementary material 1). Of them, 10 belonged to *Laurencia*, one to *Laurenciella*, one to *Osmundea*, five to *Palisada*, and two to *Yuzurua* (one of them with two varieties). Only three species were found in at least 78% of the ecozones (six and seven ecozones), while five were recorded in just one.

Ecozones VII and VIII showed the highest number of taxa, with 12 species each (Fig. 1A). *Laurencia* was the richest genus, in all cases, while *Laurenciella* and *Osmundea* were the poorest (Supplementary material 2, Figs. S1-S4). The studied areas showed a similarity between 14.3 and 73%.

The similarity analysis based on the presence and absence of species of the *Laurencia* complex in the ecozones showed two large groups, A and B (Fig. 2). Both groups were established at 30% similarity due to the 100% replacement supported for the first node, inferring greater robustness and reliability in the dendrogram separation. The cophenetic correlation (82%) indicated a high correlation between the distances of the simulated matrix and the real matrix.

Group B included ecozones II and VI with 36% similarity, while the other ecozones were found in group A (Fig. 2). Within this last group, ecozones IV and VIII showed the greatest similarity between them (80%) and with ecozone VII (73%). Ecozones III and V also showed greater than 50% similarity. Cluster analysis, revealed

Name	Province	Ecozones	Significance	Management category	Occurrence points	(Number of) Taxa
Península de Guanahacabibes	Pinar del Río	V, VI	National	Protected Area with Managed Resources	6	(6) *Laurencia caraibica, L. intricata, L. microcladia, Palisada cervicornis, P. perforata, Yuzurua iridescens*
Cayos Las Cayamas - Los Guzmanes	Artemisa	IV	Local	Faunal Refuge	5	(4) *Laurencia intricata, L. microcladia, Palisada corallopsis, Yuzurua poiteaui* var. *poiteaui*
Ensenada de Portier-Lamas	La Habana	VII	Local	Protected Natural Landscape or Seascape	2	(2) *Laurencia dendroidea, Palisada perforata*
Rincón de Guanabo	La Habana	VII	Local	Protected Natural Landscape or Seascape	7	(7) *Laurencia caduciramulosa, L. dendroidea, L. minuscula, Palisada corallopsis, P. perforata, Yuzurua iridescens, Y. poiteaui* var. *gemmifera*
Bacunayagua	Matanzas - Mayabeque	VII	Local	Ecological Reserve	1	(1) *Laurencia caraibica*
Cayo Mono-Galindo	Matanzas	VIII	Local	Ecological Reserve	4	(4) *Laurencia intricata, L. obtusa, Yuzurua poiteaui* var. *poiteaui, Y. poiteaui* var. *gemmifera*
Península de Zapata	Matanzas	III, IV	National	Protected Area with Managed Resources	4	(3) *Laurencia dendroidea, Palisada perforata, Yuzurua poiteaui* var. *gemmifera*
Ensenada de Rancho Luna	Cienfuegos	III	Local	Natural Outstanding Landscape	2	(2) *Laurencia intricata, Palisada perforata*
Las Picúas-Cayo Cristo	Villa Clara	VIII	National	Faunal Refuge	6	(6) *Laurencia intricata, L. microcladia, L. obtusa, Palisada perforata, Yuzurua poiteaui* var. *poiteaui, Y. poiteaui* var. *gemmifera*
Lanzanillo-Pajonal-Fragoso	Villa Clara	VIII	National	Faunal Refuge	10	(5) *Laurencia intricata, L. obtusa, P. perforata, Yuzurua poiteaui* var. *poiteaui, Y. poiteaui* var. *gemmifera*
Buenavista	Sancti Spíritus - Villa Clara	VIII	National	Protected Area with Managed Resources	8	(5) *Laurencia intricata, L. obtusa, Palisada corallopsis, P. perforata, Yuzurua poiteaui* var. *poiteaui*
Humedales del Norte de Ciego de Ávila	Ciego de Ávila	VIII	National	Protected Area with Managed Resources	8	(4) *Laurencia dendroidea, L. intricata, Palisada perforata, Yuzurua poiteaui* var. *poiteaui*
Jardines de la Reina	Camagüey - Ciego de Ávila	II	National	National Park	6	(5) *Laurencia filiformis, L. intricata, L. obtusa,* *Laurenciella* sp., *Yuzurua iridescens*
Humedales de Cayo Romano	Camagüey	VIII	National	Protected Area with Managed Resources	2	(2) *Laurencia intricata, Yuzurua poiteaui* var. *poiteaui*
Cayo Sabinal	Camagüey	VIII	Local	Protected Area with Managed Resources	1	(1) *Palisada perforata*
Caletones	Holguín	IX	National	Ecological Reserve	3	(3) *Laurencia dendroidea, Palisada flagellifera, P. perforata*
Reserva de Biosfera Baconao	Santiago de Cuba - Guantánamo	I	National	Protected Area with Managed Resources	4	(2) *Osmundea coelenterata, Palisada perforata*
Sur de la Isla de la Juventud	Isla de la Juventud	IV	National	Protected Area with Managed Resources	8	(6) *Laurencia chondrioides, L. dendroidea, L. intricata, L. microcladia, Yuzurua poiteaui* var. *poiteaui, Y. poiteaui* var. *gemmifera*

Tabla 1. Áreas marinas protegidas dentro de la plataforma cubana con ocurrencia de taxones del complejo *Laurencia*. Ecozonas: I: Sureste, II: Centro Sur (Jardines de la Reina), III: Sur del Macizo Guamuhaya, IV: Batabanó-Canarreos, V: Suroeste de Guanahacabibes, VI: Noroeste (Los Colorados), VII: Habana - Matanzas, VIII: Centro Norte (Sabana-Camagüey), y IX: Noreste.

Table 1. Marine protected areas within the Cuban shelf with the occurrence of taxa of the *Laurencia* complex. Ecozones: I: Southeast, II: South Central (Jardines de la Reina), III: South of the Guamuhaya Massif, IV: Batabanó-Canarreos, V: Southwest of Guanahacabibes, VI: Northwest (Los Colorados), VII: Habana - Matanzas, VIII: North Central (Sabana-Camagüey), and IX: Northeast.

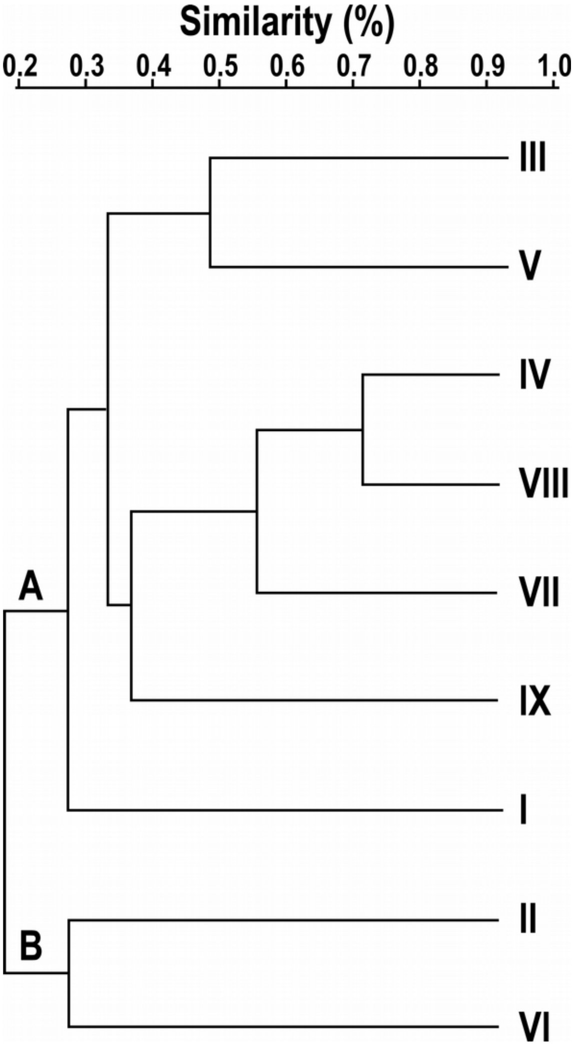

Figura 2. Dendrograma de similitud resultante del análisis de conglomerado de las ecozonas en las que se dividió la plataforma cubana, con registros de especies del complejo *Laurencia*. I: Sureste; II: Centro Sur (Jardines de la Reina); III: Sur del Macizo Guamuhaya; IV: Batabanó-Canarreos; V: Suroeste de Guanahacabibes; VI: Noroeste (Los Colorados); VII: Habana - Matanzas; VIII: Centro Norte (Sabana-Camagüey); IX: Noreste.

Figure 2. Similarity dendrogram resulting from the conglomerate analysis of the ecozones into which the Cuban shelf was divided, with records of species of the *Laurencia* complex. I: Southeast; II: South Central (Jardines de la Reina); III: South of the Guamuhaya Massif; IV: Batabanó-Canarreos; V: Southwest of Guanahacabibes; VI: Northwest (Los Colorados); VII: Habana - Matanzas; VIII: North Central (Sabana-Camagüey); IX: Northeast.

that ecozones I and IX had the least similarity with the rest.

ANOSIM analysis did not reveal any significant difference between the two groups established in the similarity analysis (R=0.03; p=0.20), suggesting that the species composition was not an excluding factor between both groups.

SIMPER results indicated that the maximum average dissimilarity between the groups was 62.18%. CLUSTER analysis showed that *Laurencia dendroidea* J. Agardh and *Laurencia microcladia* Kützing (both with 7.21%), *Yuzurua poiteaui* var. *poiteaui* (J.V. Lamouroux) Martin-Lescanne (7.13%), and *Laurencia caraibica* P.C. Silva (7.07%) were the species that most contributed to the dissimilarity between Groups A and B.

PERMDISP test for the structure and species composition of the *Laurencia* complex showed significant differences (F=7.44; p<0.01) in the dispersion between ecozones. In this sense, pairwise comparisons indicated significant differences between ecozones IV and VIII with I, III, and V (p<0.0001) and II, VI, and VII (p<0.01). In addition, ecozones VII and IX differed significantly from the rest of the ecozones (p<0.01). Non-metric multidimensional scaling confirmed the separation of ecozones II and VI from the other ecozones (Fig. 3). The ecological distance between ecozones IV and VIII was smaller than the other ecozones.

Of the 196 occurrence points for the *Laurencia* complex on the Cuban shelf, 87 were found within MPAs, mostly (73%) in those of national significance (Table 1, Fig. 1B). Lanzanillo-Pajonal-Fragoso refuge, in ecozone VIII and the area of resources, managed south of Isla de la Juventud, in ecozone IV, had the highest number of occurrence points and taxa (10, 5 and 8, 6, respectively). In contrast, smaller protected areas (Bacunayagua and Cayo Sabinal) usually had a few occurrence points and taxa. However, Rincón de Guanabo in ecozone VII was an exception. Despite its small area, it accounted for seven occurrence points from seven taxa (Fig. 1B). This ecozone also showed the single records of *Laurencia caduciramulosa* Masuda & S. Kawaguchi and *Laurencia minuscula* Schnetter within protected areas. Furthermore, *L. dendroidea*, *Laurencia intricata* J.V. Lamouroux, *Palisada perforata* (Bory) K.W. Nam, *Yuzurua poiteaui* var. *poiteaui*, and *Yuzurua poiteaui* var. *gemmifera* (Harvey) M.J. Wynne were recorded in at least five protected areas. In contrast, *Laurencia brongniartii* J. Agardh and *Palisada furcata* (Cordeiro-Marino & M.T. Fujii) Cassano & M.T. Fujii showed no records within protected areas.

The PAE tree, resulting from 31 equally parsimonious trees (CI=0.50 and RI=0.66), identified a large area of endemism that encompasses two smaller areas: A2 and B6 (Fig. 4). This large area of endemism mainly covered the Western and Central regions of the Cuban archipelago on both

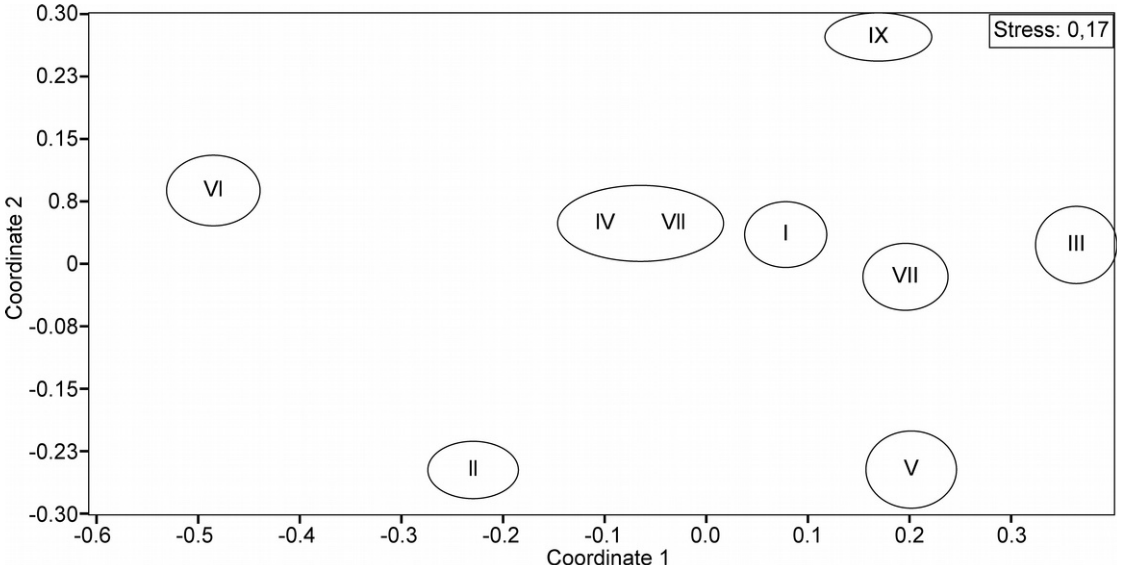

Figura 3. Escalado multidimensional no métrico (nMDS) de las ecozonas en las que se dividió la plataforma cubana y las especies del complejo *Laurencia*. I: Sureste; II: Centro Sur (Jardines de la Reina); III: Sur del Macizo Guamuhaya; IV: Batabanó-Canarreos; V: Suroeste de Guanahacabibes; VI: Noroeste (Los Colorados); VII: Habana-Matanzas; VIII: Centro Norte (Sabana-Camagüey); IX: Noreste.

Figure 3. nMDS of the ecozones in which the Cuban shelf was divided and the species of the *Laurencia* complex. I: Southeast; II: South Central (Jardines de la Reina); III: South of the Guamuhaya Massif; IV: Batabanó-Canarreos; V: Southwest of Guanahacabibes; VI: Northwest (Los Colorados); VII: Habana-Matanzas; VIII: North Central (Sabana-Camagüey); IX: Northeast.

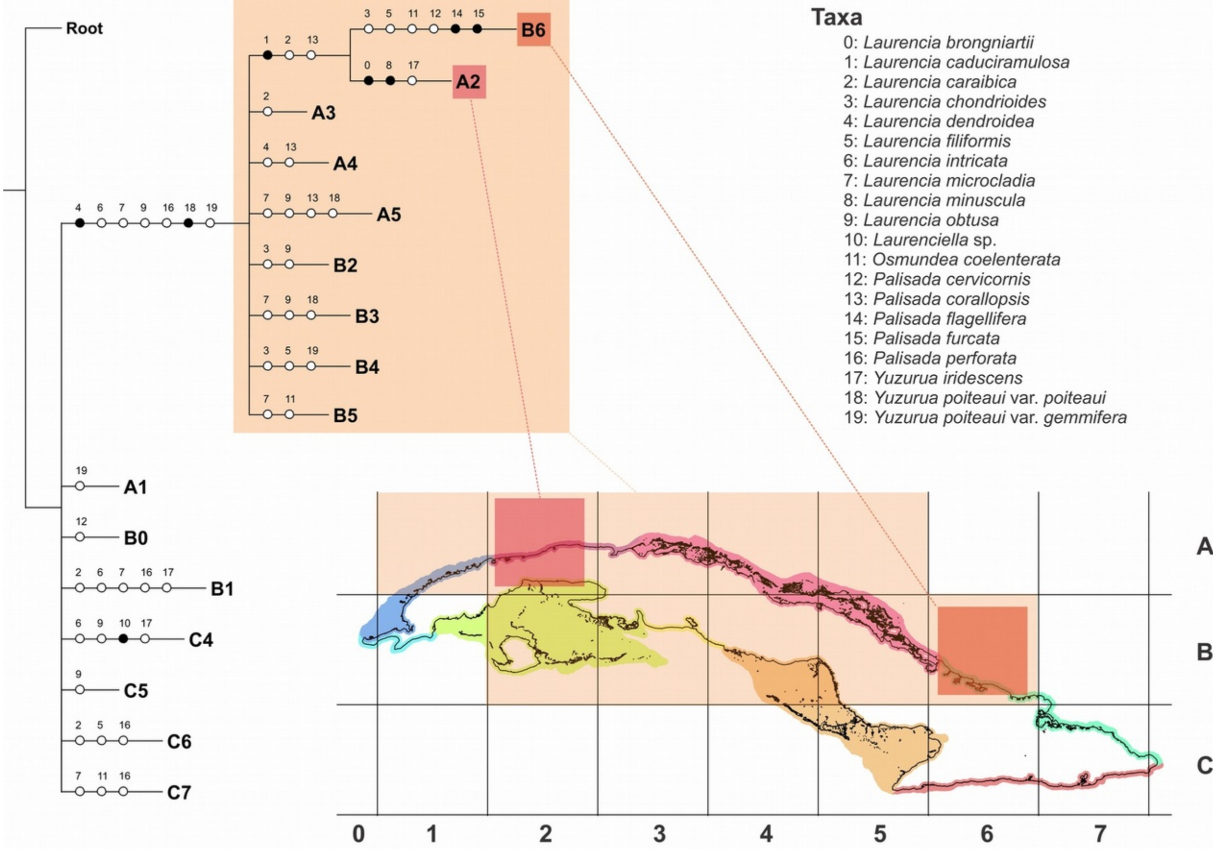

Figura 4. Árbol de consenso estricto resultante de 31 árboles igualmente parsimoniosos (IC=0,50; I0,66) en el análisis PAE. Los cuadrantes apoyados por al menos dos especies endémicas están resaltados en negro. Estas áreas están indicadas en el mapa, mostrando las zonas ecológicas reconocidas por Areces (2002). Los números sobre los círculos a lo largo de las ramas corresponden a las especies codificadas en la lista en la esquina superior derecha.

Figure 4. Strict consensus tree resulting from 31 equally parsimonious trees (CI=0.50; RI=0.66) in the PAE analysis. Quadrants supported by at least two endemic species are highlighted in black. These areas are indicated on the map, showing the ecological zones recognized by Areces (2002). Numbers above circles along the branches correspond to the species encoded in the list in the upper right corner.

shelf coasts and was supported by *L. dendroidea*, *Y. poiteaui* var. *poiteaui*, and *L. caduciramulosa*. Area A2 corresponded mainly to ecozone VII and was supported by *L. brongniartii*, *L. caduciramulosa*, and *L. minuscula*. Rincón de Guanabo was the protected area where almost all the species supporting A2 were found, except *L. brongniartii*. On the other hand, area B6, corresponded largely to ecozone IX and was supported by *Palisada*: *Palisada flagellifera* (J. Agardh) K.W. Nam, and *P. furcata*. The Eastern zones (I and IX) had the lowest number of protected areas with records of the *Laurencia* complex. Most *Palisada* species supporting B6 as an area of endemism were not recorded in any of the protected areas of these ecozones, except for *P. flagellifera* in Caletones Ecological Reserve.

Discussion

CLUSTER results indicated that the species composition had a low similarity between ecozones, showing two main groups with 30% similarity. ANOSIM test did not find any significant difference between the groups, reflecting that the species composition was not an excluding factor between them.

Despite this, the distribution of taxa within the ecozones of the Cuban marine shelf was not homogeneous, as shown by PERMDISP results and figure 3. The differences in the species number between the ecozones could be due to the variety of environments found in large areas such as ecozones II, IV, and VIII.

Similarity indices are used to identify bioregions and patterns of beta biodiversity. They are based on the number of species shared between localities but do not consider spatial or environmental proximity. Insufficient sampling due to species with limited distributions, difficult to observe or identify, would lead to false absences (Barbosa 2015). Therefore, we selected the Sørensen or Dice index, which doubles the importance of shared attributes and is helpful for more effective comparisons between rich and poor collections under conditions of great heterogeneity in the qualitative data matrix (Herrera 2000).

Another problem is the correct species identification. Recent phylogenetic studies have been useful to detect misidentifications of species records in the Atlantic Ocean, especially Florida, Venezuela, Brazil, and the Mexican Caribbean (Cassano *et al.* 2012, 2020, Sentíes *et al.* 2015, 2016, Collado-Vides *et al.* 2018). The molecular phylogenetic analysis of these species would allow us to identify new lineages in a wide distribution range, as happened with other red algal groups (Núñez-Reséndiz *et al.* 2015, Hernández *et al.* 2017, Popolizio *et al.* 2022), and better understand the historical biogeography of the *Laurencia* complex in the Atlantic Ocean.

Despite the above, ecozones IV and VIII and these with VII showed similarity greater than 70%. In addition to a spatial ecological approach between ecozones IV and VIII observed in the nMDS. Ecozones II and VI were separated with less than 40% similarity. These results partially coincide with those found by the PAE.

The greater diversity of representatives of the *Laurencia* complex in ecozones IV, VII, and VIII could be due to the variety of substrates, temperature, salinity, or other factors that regulate the development of marine flora, as well as geographical barriers or the establishment of artificial shores (Wiencke & Bischof 2012). Results of similarity in the species composition of the *Laurencia* complex between ecozones could be explained by the fact that Cuba is geographically located in a tropical region with formations of coral origin, where temperature, habitats, and substrates favor the development of many species of Ceramiales. In the Caribbean, members of the *Laurencia* complex are very abundant. They, can be found in soft and hard bottoms, and as epiphytes on other algae, seagrasses, and animals.

The north and south coasts of the Cuban shelf differ considerably (Suárez 1989b, Areces 2002, Areces & Salinas-Chávez 2020). The South coast has two large regions with a wide shelf (Batabanó-Canarreos Southwestern shelf - IV and the South Central Jardines de la Reina - II), shallow waters with reefs, mangrove keys, sand, and rocks. The northern shelf is much narrower and only at the north of Pinar del Río (Northwest Los Colorados shelf- ecozone VI) and Villa Clara-Camagüey (North Central Sabana-Camagüey shelf-VIII), it reaches about 10 miles. On the other hand, the south coast has a predominantly sandy-muddy substrate, while in the north, it is sandy and sandy-rocky of coral origin. For the entire shelf, the depth is seldom more than 25 m (Areces 2002, Areces & Salinas-Chávez 2020).

Cuba is considered a tropical island; however, its climate is not typically oceanic due to the continental influence of North America. Its temperature, light, and rainfall patterns vary depending on the time of year or the influence of climatological phenomena such as tropical storms and hurricanes, whose frequency and intensity have been modified in recent years due to climate change (Planos *et al.* 2012).

Ecozones IV, VII and VIII are large areas with diverse habitats, with IV and VIII being the widest. Ecozones IV and VIII are characterized by having all the substrates and biotopes recognized for Cuba (Jiménez & Alcolado 1990, Suárez *et al.* 2015, Cabrera *et al.* 2019). In them, the seagrasses predominate, but there are also keys and islets, coastal and of keys mangroves, and rocky coasts; coral reefs with lagoons usually bordered these ecozones. The ecozones have been one of the most studied within the marine shelf, and in the last two decades, there has been a great sampling intensity, mainly in ecozone VIII (Alcolado *et al.* 2007, Martínez-Daranas *et al.* 2007, 2021). For its part, ecozone VII has a narrow shelf without keys, with dominant intertidal and rocky subtidal biotopes. Coastal mangroves and sandy beaches with seagrasses in some reef lagoons, among other habitats, give the coastline a high algal wealth. It has also been extensively studied since the country's leading research centers are located in this ecozone, concentrating most phycologists (Suárez *et al.* 2015).

The variety of substrates is one of the factors that favored the high species richness of the *Laurencia* complex in the Cuban archipelago. Ninety-five percent of the *Laurencia* complex taxa found in Cuba have been collected from rocky or hard substrates. Taylor (1960) and Lüning (1990) pointed out that these substrates exposed to the waves host the greatest diversity of marine algae since they offer less competition with sessile invertebrates than coral reefs. Rock texture, degree of hardness, and color also influence algal communities (Areces *et al.* 2015).

Some red algae have effective adaptation mechanisms that allow them to occupy exposed habitats and avoid being uprooted by the influence of physical factors such as wave action. Some *Laurencia* species, such as *L. dendroidea* and *L. microcladia*, are fixed to the substrate through rhizoids and basal discs, which emerge from stoloniferous branches (Littler & Littler 2000, Gil-Rodríguez *et al.* 2012). Both species together with *P. perforata* were abundant and commonly observed on this type of substrate.

Meadows of *Thalassia testudinum* K.D. Koenig were common and abundant in ecozones IV and VIII. These meadows are generally found around river mouths, bays, estuaries, and coastal lagoons. Seagrasses play an essential role in stabilizing the sandy and silty substrate where algae can develop adequately, taking advantage of the spaces left free by seagrasses (Santelices 1977, Huerta 1978). Within the Cuban archipelago, these habitats are characterized by being shallow and in protected environments, with little water movement. *L. intricata* and the two varieties of *Yuzurua poiteaui* were recorded for this biotope.

In benthic marine communities, epiphytism leads to a greater number of strata and heterogeneity of habitats (Hicks 1980, Stewart 1982), potentially increasing the species diversity in these communities (Menge & Sutherland 1976, Krebs 1986, Jover *et al.* 2020). Epiphytism represents an option among colonization strategies. Epiphytic macroalgae might have advantages in the competition for light and nutrients (Wiencke & Bischof 2012), especially in the case of simpler morphofunctional types (Steneck & Dethier 1994). Mature leaves of *T. testudinum* constitute a substrate strongly colonized by algae, on which we recorded *L. caduciramulosa*, and Sentíes *et al.* (2010) found *L. minuscula*.

Suárez (1989b) carried out an ecological analysis of the macrophytobenthos of the Cuban shelf, and Suárez and Pérez (1989) analyzed the algae associated with *Rhizophora mangle* roots in the keys of Isla de la Juventud. These authors found that the order Ceramiales dominates in red mangrove roots, intertidal and rocky subtidal biotopes, coastal and of keys mangroves. Particularly referring to the epiphytism on phytobenthos in the Cuban shelf, Suárez (1989b) also found that the Ceramiales order dominates along with Bangiales. This author recorded *P. perforata* and *Laurencia obtusa* (Hudson) J.V. Lamouroux as epiphytes on the red alga *Digenea simplex* (Wulfen) C. Agardh and *L. caraibica* on *Sargassum filiforme* Montagne.

Specific richness, in general, is similar to the records made by Suárez *et al.* (2015) for Cuba and García-García *et al.* (2020) for red algae in the Mexican Atlantic. These results support the correlation that the greater the variety of habitats, the higher the richness of recorded species.

Ecozones II and VI with the lowest percentage of similarity, constitute areas of greater extension and present a wide shelf with diverse habitats, which favor the growth of marine flora, mainly in ecozone II. Despite the low species richness and the limited abundance of *Laurencia* in these ecozones, it is possible that in these areas there are a greater number of species and new records for science in Cuba. This fact was verified with the new record of the genus *Laurenciella* within the protected marine area of Cayo Anclitas in Jardines de la Reina (ecozone II).

An area of endemism is defined as the sympatric congruence between two or more endemic species, based on the fact that these species share a common spatial history (Morrone 1994, 2007). Other areas that can be documented are the secondary areas, which have only one endemic species, or the so-called relic species that are important because these areas may be later isolations where species radiation has not yet occurred (Ippi & Flores 2001, Vargas *et al.* 2008). The PAE method allows us to identify areas of endemism from area cladograms. As in phylogenetic systematics, at least two synapomorphies (restricted species) are necessary to define an area of endemism (Morrone 2014, Hernández *et al.* 2017).

The species found by the PAE supporting areas of endemism (A2 and B6) are considered rare or infrequent for Cuba (Suárez *et al.*, 2015). Greater sampling efforts are required in other protected areas of the Northwest Coast (VII) since there is a discrepancy in the number of species/occurrence points recorded in Ensenada de Portier-Lamas (2/2) and Bacunayagua (1/1) compared to Rincón de Guanabo (7/7). Considering they all belong to the same area of endemism indicated by PAE (A2), future sampling efforts could reveal richer diversity of the *Laurencia* complex in the Cuban shelf.

Eastern zones had a low number of species/occurrence points and were represented mainly by the common species *P. perforata* (Table 1). Only one species, *P. flagellifera*, which supports B6 as an area of endemism, was recorded within a protected area Caletones. Therefore, for the area of endemism B6, both sampling and conservation efforts are necessary.

Despite being close to the capital city of Cuba, the MPA of Rincón de Guanabo has diverse ecosystems (rocky bottoms, sandy bottoms with seagrass patches, and coral reefs) where multiple communities live or seek refuge, giving it a high equity value. Based on our results, we propose to change the significance level of Rincón de Guanabo from Local to National, since it has a high diversity not only of species of the *Laurencia* complex but also of other important biological groups in the ecosystem (Alcolado 1989, Castellanos *et al.* 2004, Caballero *et al.* 2009, Hernández-Delgado *et al.* 2017, Gómez *et al.* 2019). In the case of Caletones Ecological Reserve, we propose that its status as MPA be analyzed and finally approved for its administration and management by the Integral Forestry Company (EFI) (see Table 1 in Perera Valderrama *et al.* 2018).

Suárez & Martínez-Daranas (2020) analyzed the marine phycoflora from tropical and subtropical western Atlantic areas. These authors found that the Cuban phycoflora has greater than 70% similarity with some of the ecoregions defined by Spalding *et al.* (2007) for the Tropical Northwestern Atlantic provinces, such as Florida, the southern Gulf of Mexico, the Western Caribbean, and the Southwestern Caribbean. This high similarity could be due to the location of Cuba in the center of the analyzed region, the increase in information on the macroalgae species in the different areas, changes in the regional phycoflora resulting from the dispersion of diasporas within the same phytogeographic province, the connectivity of oceanic waters or anthropic causes such as naval traffic and aquariums.

The Caribbean Sea is the Atlantic area with the highest species richness of *Laurencia* (22 spp, Guiry & Guiry 2022). Hernández *et al.* (2017) referred to some of these endemic species that inhabit this region, such as *Laurencia laurahuertana* Mateo-Cid, Mendoza-González, Sentíes & Díaz-Larrea in the western Caribbean, *Laurencia foldatsii* N. Rodríguez Ríos in the southern Caribbean, *Laurencia chondrioides* Børgesen, and *L. minuscula* in the Caribbean Sea. Recently, Popolizio *et al.* (2022) recorded the new species *Chondrophycus planiparvus* Popolizio, C.W. Schneider & C.E. Lane as endemic to Bermuda. This biogeographic pattern is also shared by the diversity distribution of several unrelated taxa, such as coastal fishes, mangroves, coral reefs, and seagrasses in the Atlantic Ocean (Tittensor *et al.* 2010).

The Northwestern Atlantic, Europe, and the Caribbean Sea share species of the *Laurencia* complex with other regions such as the Indo-Pacific. For example, *P. flagellifera*, whose type locality is in the Indian Ocean, can be considered as a pantropical species with amphi-Atlantic distribution having been recorded from Cuba (Areces *et al.* 2003), Brazil (Fujii *et al.* 2006) and the Canary Islands (Gil-Rodríguez *et al.* 2010).

In addition, Brown & Lomolino (1998) found other areas of endemism in the south Atlantic, such as in Brazil, the Gulf of Guinea, and South Africa. The Gondwana breakup is the geological process that explains this endemism (Hernández *et al.* 2017).

Sentíes & Fujii (2002), Fujii & Sentíes (2005), Gil-Rodríguez *et al.* (2012), Machín-Sánchez *et al.* (2014, 2018) and Hernández *et al.* (2017) documented the spatial distribution patterns of the *Laurencia* complex in the Atlantic region. Although *Laurencia*, *Palisada*, *Osmundea*, and *Yuzurua* have a wide distribution in the different regions and corresponding oceans, other genera such as *Chondrophycus*, *Laurenciella*, *Ohelopapa*, and *Corynecladia* are restricted to a particular region (Guiry & Guiry 2022). The *Laurenciella* species have so far been recorded for the Atlantic Ocean and the Mediterranean Sea (Gil-Rodríguez *et al.* 2009, Cassano *et al.* 2012, Collado-Vides *et al.* 2018, Israel *et al.* 2020, Serio *et al.* 2020). On the other hand, *Chondrophycus*, *Corynecladia*, and *Ohelopapa* were found predominantly in the Indo-Pacific region, with few records in the Atlantic (Guiry & Guiry 2022). Of these genera, only *Ohelopapa flexilis* (Setchell) F. Rousseau, Martin-Lescanne, Payri & L. Le Gall, and *Chondrophycus anabeliae* Sentíes, M.T. Fujii, Cassano & Dreckmann have been reported for the Mexican Atlantic (Sentíes *et al.* 2016, Pedroche & Sentíes 2020). More recently, Cassano *et al.* (2020) found the latter species in Venezuela and Popolizio *et al.* (2022) recorded a new species of *Chondrophycus* (*C. planiparvus*) in Bermuda, which represents an expansion of the distribution of the genus toward northern Atlantic subtropical areas. *O. flexilis* was also quoted from Spain and the Canary Islands within the Atlantic (Guiry & Guiry 2022).

Conclusions

Our knowledge about the *Laurencia* complex in the Cuban archipelago is still insufficient, reflected in the differences in the species richness and distribution found within the shelf. The macroalgae of this complex differ between environments of the Cuban marine shelf. The characteristics of the substrate and associated benthos combined with the circulation patterns of ocean currents are probably some of the factors that determine the composition and distribution patterns of the *Laurencia* complex in Cuba. All these factors reinforce the need for a more exhaustive and comprehensive review of the *Laurencia* complex in the Cuban archipelago, carried out by a greater number of specialists, mainly in those less known areas such as the southern coast and the eastern region. Consequently, the incorporation of molecular characters to diversity studies considering a greater number of genera within the complex will increase the alpha diversity. MPAs are excellent refuges to preserve many species from extinction, including the macroalgae of the *Laurencia* complex. Given the above, the need for constant floristic monitoring along the coasts is imperative, particularly due to the large number of protected areas found in the Cuban archipelago.

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Appendix

This article includes the following electronic supplementary information:

Table S1: https://www.um.es/analesdebiologia/numeros/44/PDF/44_2022_06_SM1.pdf

Figures S1-S4: https://www.um.es/analesdebiologia/numeros/44/PDF/44_2022_06_SM2.pdf