Drivers of community structure and habitat suitability in ponds of the New Caledonia biodiversity hotspot

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ABSTRACT

Despite being present on all continents including Antarctica, ponds remain an understudied freshwater ecosystem. Ponds are particularly diverse in their physicochemical characteristics which is reflected in the biological assemblages inhabiting them. On the New Caledonia archipelago, acknowledged to be a global biodiversity hotspot, lentic freshwater habitats are numerous. The archipelago is subjected to extremely diverse environmental conditions notably divided along two approximate axes. The north-east has high precipitation rates for the most part (around 3000 mm/y), while the west coast has low precipitation rates (around 900mm/y). On a practically perpendicular axis, the south-east has soils with high heavy metal concentration while it is low in the north-west. We analysed the crustacean species inhabiting small lentic freshwaters and delineated two major assemblages with network clustering analyses. We then modelled the distribution drivers of these communities and identified heavy metal soils and annual precipitation rates as the major drivers. Our models allowed us to project the distribution of suitable areas for each assemblage and suggest the existence of a buffer area between the two assemblages.

Keywords: freshwater, zooplankton assemblages, network analyses, distribution models, ultramafic massifs, precipitation, mining activity

Introduction

Small lentic freshwater habitats, here designated as ponds, are ubiquitous throughout all climatical regions and cover a greater area of the Earth surface than lakes (Downing et al., 2006; Williams, 2006). Despite this prevalence, ponds are significantly more fragmented in their distribution. They represent a diverse and dynamic habitat that exhibits considerable spatial and temporal heterogeneity. Indeed, a number of variables, including pH, trace element concentration, turbidity and deepness, are dependent on a range of geographical characteristics, such as soil type and topography, as well as temporal factors, such as recent evaporation rates and precipitation levels (Tavernini, 2008; Williams, 2006). These environments are nonetheless understudied in comparison to other surface freshwater environments such as lakes or rivers, especially in tropical regions (Faghihinia et al., 2021; M. J. Hill et al., 2021).

A large proportion of ponds worldwide undergo cyclic drying which has profoundly structuring influence on the biota. The persistence of populations in temporary ponds implies necessary drought survival traits, such as diapausing eggs (Brock et al., 2003; Incagnone et al., 2015; Williams, 2006). Furthermore, the habitat duration, also called hydroperiod, is a crucial factor influencing populations and communities inhabiting temporary ponds (Olmo et al., 2016; Schneider & Frost, 1996; Tavernini, 2008). For instance, a species that attains maturity 13 days after the pond is flooded such as *Lynceus biformis* would not be observed in a temporary pond with a 10-day hydroperiod (Wang et al., 2014). As modelled by Macedo et al., (2024), many micro-crustacean species inhabiting ponds are not described, especially in temporary waters. Such Linnean shortfall in continental micro-crustacean induces the six other shortfalls described by Hortal et al., (2015), highlighting the depth of our current knowledge gaps regarding these organisms. In New Caledonia, most species of micro-crustaceans are known from less than 6 locations, and in many cases, just a single one (Longhurst, 1955; Olesen et al., 2016; Timms, 1985).

Communities of crustacean species in ponds are highly reliant on all aforementioned variables of the environment (Feld et al., 2016). In this article, we describe crustacean species assemblage which is defined as a multi-specific group of taxonomically related populations that occur in a given space (Stroud et al., 2015). In New Caledonia, lentic freshwater crustacean assemblages are notably composed of *e.g.*, the endemic longtail tadpole shrimp sub-species *Triops longicaudatus intermedius* (Longhurst, 1955), of the recently described copepod *Boeckella sibleti* (Royaux et al., 2024), of the globally distributed Ostracoda species *Candonocypris novaezelandiae* (Martens et al., 2019), and of the remarkable Australian-New Caledonian water flea *Daphnia longicephala* (Timms, 1985). Lentic freshwater micro-crustaceans have never been studied from the perspective of species assemblages on the archipelago.

Nouvelle-Calédonie (New Caledonia, Kanaky) is an archipelago located in the southwest Pacific Ocean. Its main island, Grande Terre, is continental and separated from Australia approximately 105 Mya (Maurizot & Campbell, 2020). The archipelago is known for its outstanding biodiversity and has one of the highest proportions of endemic species on earth (Veron et al., 2019). In New Caledonia, mean annual precipitation rates exhibit a considerable range over the territory, from 887 to 3339 mm, which results to markedly disparate conditions in the numerous permanent and temporary ponds that are distributed over the archipelago. The density of lentic freshwaters is notably high in the extreme south of Grande Terre in the Plaine des Lacs and the Parc Provincial de la Rivière Bleue, which has been designated a “wetland of international importance” under the Ramsar Convention (Jeanpert et al., 2016). This area is also notable for its heavy metal-rich soils, which originate from the alteration of ultramafic massifs. Such massifs cover approximately one-third of the archipelago and are considered as a significant factor in environmental filtering there (Isnard & Jaffré, 2024; Zakardjian et al., 2023). Indeed, a significant proportion of endemic species of the archipelago are known to be exclusively found in ultramafic environments (Nattier et al., 2013; Pillon et al., 2021). However, the high concentrations of notably nickel, cobalt, and chromium in ultramafic rocks and soils are an important economic resource for the archipelago. The mining activity on ultramafic massifs is present in Grande Terre and surrounding islands since the 19th century, which has many impacts on landscapes and

ecosystems (Boula et al., 2022; Germande et al., 2022; Pascal et al., 2008). Freshwaters are particularly sensitive to mining and other anthropogenic perturbations, which have led them to be considered among the most vulnerable environments in terms of biodiversity (García-Girón et al., 2023; Tickner et al., 2020). Indeed, in New Caledonia, many ponds are notably found in and around mining facilities, the largest being the Prony Resources mine in the Plaine des Lacs. This facility extracts nickel from soils with a rather low heavy metal concentration. The process inevitably produces many chemical residuals which pollutes freshwaters (Germande et al., 2022). In addition to evident impact through the excavation of soils, it creates inert wastes in the form of fine dust that is filling local freshwaters (Boula et al., 2022). Beside mining activity, the agricultural practice and frequent wildfires caused the plant cover to be considered "modified" for 40% of the territory (Isnard & Jaffré, 2024). The modification of plant covers inevitably has heavy impacts on the distribution and characteristics of freshwaters (Reid et al., 2019; Stocker et al., 2023). These threats are particularly significant for pond micro-crustaceans inhabiting freshwater islands on dry oceans they cannot cross on their own (Incagnone et al., 2015).

Based on 70 samples of crustaceans from freshwater ponds on the archipelago, we provide new records of species that were unknown in New Caledonia, contributing to decrease the Wallacean knowledge shortfall (*i.e.*, gaps in the known geographic distribution of species; Hortal et al., 2015). We computed a biogeographical network of these 70 samples to investigate whether several assemblages could be delineated. Then, we sought for potential drivers of the distribution of these delineated assemblages using correlative modelling and projected the suitable distribution of each assemblage on the archipelago. Additionally, the sampling completeness and diversity estimates at several diversity orders are evaluated to account for the accuracy of the assemblage delineation and their composition in rare, frequent, and highly frequent species. The results of these analyses could provide insight into the extent of the Linnean knowledge shortfall that remains to be addressed regarding these species.

Material and methods

Sampling and identification

Samples were collected on the New Caledonian archipelago during three "La Planète Revisitée" campaigns between 2016 and 2018 and, by the environmental consulting firm "Ethyco" and the organisation "Vies d'Ô douces" between 2020 and 2023. During these sampling expeditions, 535 locations were visited. However, a significant proportion of these were found to be dry, and thus 65 were sampled using a plankton net (NHBS, Bonn, Germany) with a frame diameter of 25 cm and a 55 cm-long bag of 200 µm nylon mesh with a filter at the tip. The content of the filter is preserved in 80-90% ethanol.

In total, 70 samples were collected from the 65 locations and we entirely sorted their content to identify the species of crustaceans (fig. 1; supplementary tab. S1). We based identifications under binocular microscope (and optical microscope when required) on keys by El-moor Loureiro (1997), Korovchinsky (2001), Quinlan & Bayly (2017), Smirnov & Timms (1983), Stingelin (1915), and Timms (1985). We pooled all individuals of the same species and from the same sample in clean 80-90% ethanol in a glass tube with a screw cap and identification were verified by 2-3 different persons.

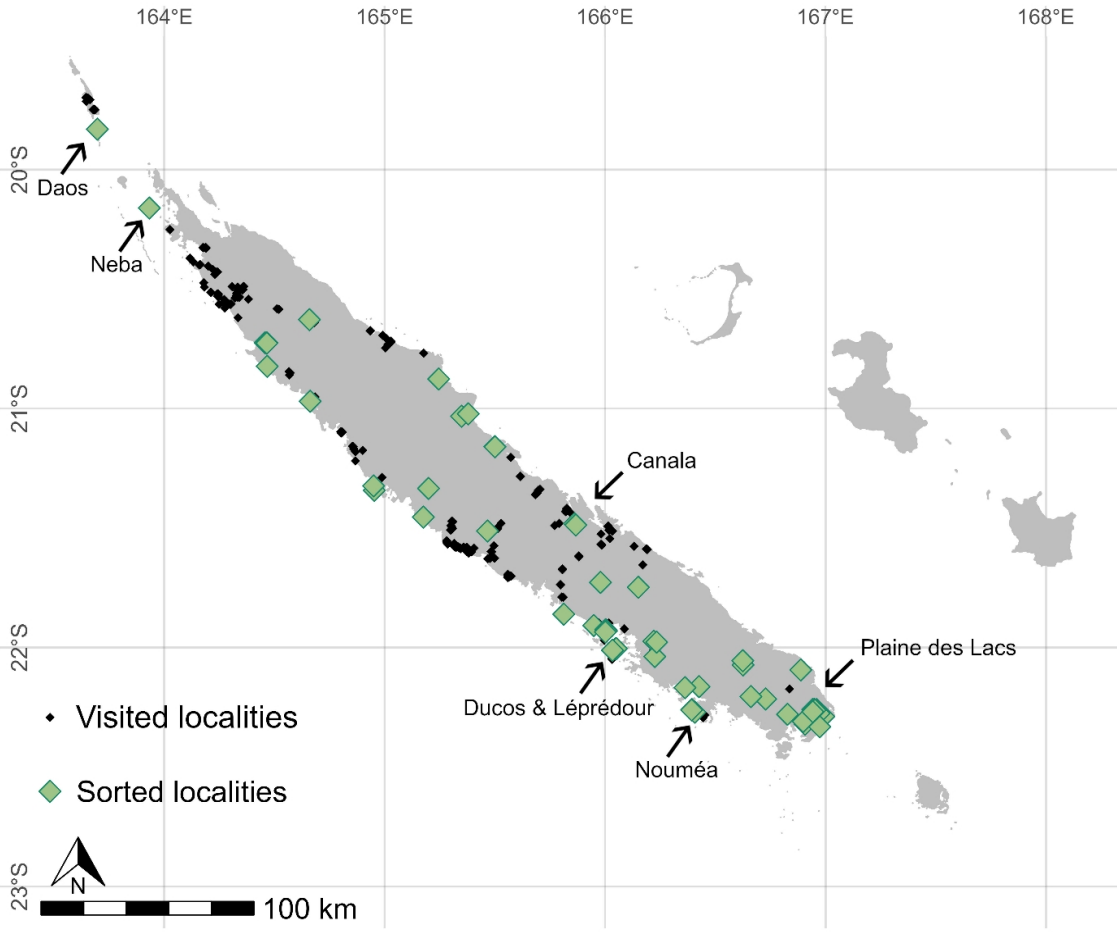

Figure 1 - Visited and sorted localities.

Assemblage delineation

For the assemblage delineation analysis, we applied several filters on raw data. We removed identifications of class Ostracoda and of orders Cyclopoida and Harpacticoida as for these taxa the formal identification requires damaging individuals with micro-dissections. The taxonomy of the family Chydoridae has experienced many changes and re-arrangements in the past decades (Gu et al., 2022; Sinev & Dumont, 2016; Smirnov, 1971; Van Damme et al., 2010). As most of the Chydoridae species we identified in the samples were not recently revised, identifications of this family were ambiguous and we removed them from the data. Additionally, individuals identified from the genus *Ilyocryptus* seemed to present features from two morphologically close species *I. sordidus* and *I. spinifer* (Kotov & Elias-Gutierrez, 2009). As the two were undistinguishable, we removed identifications of this genus as well. Finally, we did not consider identifiable moults and resting stages as a presence of the related species in the analysis.

To cluster samples into assemblages, we used a bipartite species-sample network which is designed with nodes and links, each node can represent a species or a sample. When a species occurs in a particular sample, the node of the species is bound with the node of the sample through a link. In this kind of bipartite network, direct species-species or sample-sample links are not allowed. Assemblages were delimited on the network with a hierarchical clustering algorithm with 1000 trials and 1000 draws of random seeds using the R 4.2.2 package bioregion 1.1.1 and the Map equation algorithm infomap 2.7.1 (Bloomfield et al., 2018; Leroy et al., 2019; Rosvall & Bergstrom, 2008; Vilhena & Antonelli, 2015). The clustering algorithm is delineating assemblages with high intra-group and low inter-group connectivity - in other words, it groups species that co-occur frequently, keeping each cluster distinct from others in terms of species co-occurrence. If the assemblages are spatially nested, Map Equation will uncover a hierarchical clustering structure:

the top-level divisions represent the most distinct clusters, while subsequent, finer levels reveal sub-assemblages nested within those larger groups. We chose this network approach due to its reliability even with low species richness, and because it preserves the identity of the species throughout the whole clustering process, as opposed to methods that transform species identity into β diversity (Leroy et al., 2019; Victorero et al., 2023).

We graphically represented the final network with Gephi 0.9.2 (Bastian et al., 2009) and the forceatlas2 algorithm that groups interconnected nodes together and separates less connected nodes. We reworked the final representation of the network for better clarity using Inkscape 1.2.2 (The Inkscape Project).

Sampling completeness and diversity estimates

For each assemblage delineated with the bipartite network, we computed sampling completeness and diversity estimates using the interpolation and extrapolation for three dimensions of biodiversity method based on Hill numbers (Chao et al., 2020; M. O. Hill, 1973; Ramiro-Sánchez et al., 2023). Hill numbers characterise the diversity of species with equal frequencies depending on the q parameter and, although typically computed on abundance data, they can also be computed on occurrence data as this is the case here. Hence, each order q = 0, q = 1, and q = 2 corresponds to the estimation of the total species richness, the number of frequent species and the number of highly frequent species respectively (see Chao et al., 2020). We computed estimates of Hill numbers at the three orders on the whole dataset and on delimitations based on the previously delineated assemblages using the R 4.2.2 packages iNEXT.3D 1.0.4 and iNEXT.4steps 1.0.0 (Chao & Hu, 2024). Sampling completeness estimation is critical to validate the delineated assemblages and identify lacks in the dataset. Estimated Hill numbers permit us to better comprehend each delineated assemblage and compare their characteristics.

Assemblage distribution modelling

We modelled the relationships between the distributions of the assemblages and their environment in order to identify the main drivers influencing these distributions and to map suitable areas for each assemblage across the archipelago. We considered a given assemblage to be present in a location when at least one of its samples has been associated with it, and absent when none of its samples has been associated with it. When two samples from the same location were associated with two different assemblages, we considered the two assemblages were present. We tested four response variables to model the potential distribution of each assemblage. The presence of ultramafic soils is known to be highly structuring for species and assemblages on the New Caledonian archipelago (Isnard & Jaffré, 2024; Nattier et al., 2013; Pillon et al., 2021). The annual precipitation amount is considered here as a proxy of habitat duration of freshwater ecosystems (Tavernini, 2008) and the distance to freshwater as a proxy of habitat presence probability. Finally, the samples examined in this article were not destined to such analyses and the sampled habitats exhibited varying degrees of accessibility, resulting in localised patchy sampling. Consequently, it seemed critical to take account of sampling density to model the potential distribution of delimited assemblages.

We retrieved spatial data layers for the presence of ultramafic massifs (fig. 2a; peridotite v23-09-2021; https://georep-dtsi-sgt.opendata.arcgis.com/datasets/dtsi-sgt::massifs-de-p%C3%A9ridotites-au-50-000-2), the annual precipitation amount (fig. 2b; CHELSA 2.1, https://chelsa-climate.org/bioclim/) and the distance to freshwater based on the global maximum water extent (fig. 2d; 1984-2021, European Commission, https://global-surface-water.appspot.com/; Pekel et al., 2016) on online open data repositories. In addition, we computed the sampling density (kernel) of all campaigns with R 4.2.2 package MASS 7.3-58.1 (fig. 2c).

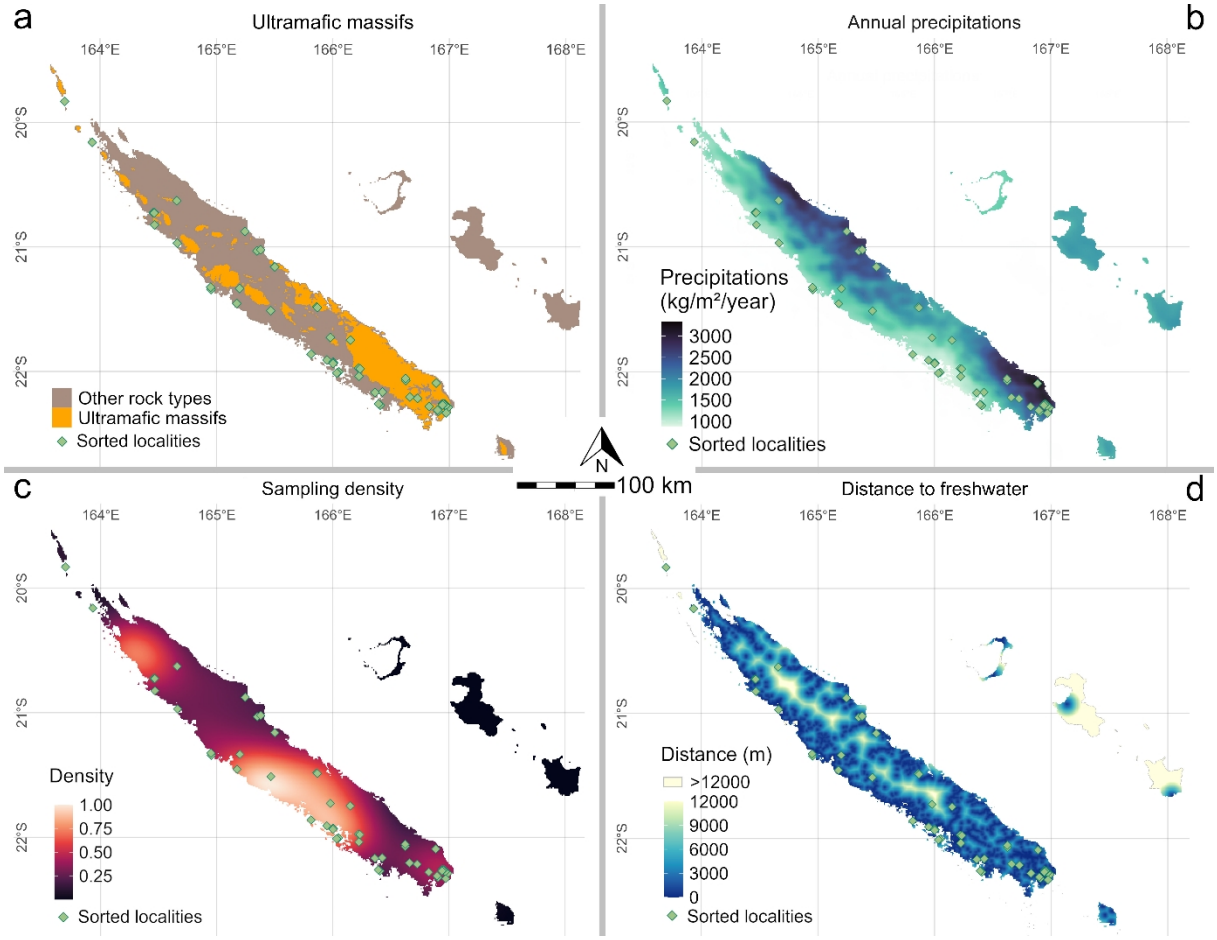

Figure 2 - Map of sorted localities and response variables tested for the assemblage distribution models. Presence-absence of ultramafic massifs (a); annual precipitation modelled by CHELSA (b); expeditions' sampling kernel density (c); and distance to freshwater derived from the global maximum water extent (d).

We found no correlation between all four variables according to Pearson's coefficient (supplementary data S2). The final environmental stack had 0.0083 × 0.0083 degree resolution. We calibrated and computed assemblage distribution models on geographically filtered occurrences using mostly R 4.2.2 packages terra 1.7-71 and biomod2 4.2-4.

We modelled assemblage-environment relationships with machine-learning models using parameters recommended in the comprehensive modelling benchmark recently published (Valavi et al., 2021). Specifically, we computed Random Forests (RF; Breiman, 2001; Valavi et al., 2021), Generalised Boosted Regression Models (GBM; Ridgeway, 1999), and extreme Gradient Boosting models (XGBOOST; Chen & Guestrin, 2016), each with five runs of random cross-validation calibrated on 80% of the dataset. We evaluated each model based on 20% of the dataset using TSS, ROC and Jaccard estimates. We chose model parameters (see supplementary data S2 and S3) to down-sample RFs and down-weight GBMs and XGBOOST to balance the statistical contribution of presences and absences in the models (Guisan et al., 2017; Valavi et al., 2021). We selected final models on the basis of their performance (TSS, ROC, and Jaccard estimates; supplementary data S2) as well as their complexity, favouring models with the lowest complexity in response curves (*i.e.* smooth trace), given that our small number of occurrences would inevitably lead to overfitting for complex models (Merow et al., 2014).

For each assemblage, we used the mean suitability of all individual assemblage models to define a binary map representing the most suitable assemblage at each pixel. Additionally, we produced a map of the average suitability of the most suitable assemblage to estimate the level of certainty of the binary map.

We applied the ODMAP protocol to reproducibly report our modelling protocol (Zurell et al., 2020). It is available in supplementary material (supplementary data S3). The complete analytical workflow from data preparation and assemblage delineation to final assemblage distribution models is available in supplementary data S2 along with associated data. Scripts are available on Github (https://github.com/ColineRoyaux/BioCommunity; https://github.com/ColineRoyaux/cleanSIG; https://github.com/ColineRoyaux/DM).

Results

Identification and assemblage delineation

In total, we identified 24 species of 13 genera in the 70 samples (tab. 1). The highest species richness was found in HYNC4002 with 6 species detected and most locations had a species richness of 1 (n=32) or 2 (n=17). The full dataset for this study is available on the Data.InDoRES platform (https://doi.org/10.48579/PRO/CD4FC4; Royaux *et al*., 2026).

Table 1 - Species identified in sorted samples, their occurrence count (N), assemblage associated with them using the network clustering algorithm, the assemblages associated with the samples in which they were observed and their known distribution.

Class	Order	Family	Species	N	Associated assemblage	Observed in samples from	Known distribution
Branchiopoda	Anostraca	Streptocephalidae	*Streptocephalus archerii*	8	Assemb. 1	Assemb. 1	Australia; New Caledonia
	Notostraca	Triopsidae	*Triops longicaudatus intermedius*	1	Assemb. 1	Assemb. 1	New Caledonia
	Anomopoda	Daphniidae	*Ceriodaphnia rigaudi*	10	Assemb. 1	Assemb. 1	Southern hemisphere
			Daphnia cephalata	3	Assemb. 1	Assemb. 1	Indopacific area
			Daphnia longicephala	2	Assemb. 1	Assemb. 1	Australia; New Caledonia
			Simocephalus exspinosus australiensis	4	Assemb. 1	Assemb. 1 & 2	Australia; New Caledonia
			Simocephalus acutirostratus	3	Assemb. 1	Assemb. 1	Southern hemisphere
		Macrothricidae	*Macrothrix triserialis*	1	Assemb. 1	Assemb. 1	Southern hemisphere
			Macrothrix spinosa	10	Assemb. 1	Assemb. 1	Southern hemisphere
			Macrothrix sp. A	5	Assemb. 2	Assemb. 2	New Caledonia
		Moinidae	*Moina micrura*	6	Assemb. 1	Assemb. 1	Global
	Ctenopoda	Sididae	*Diaphanosoma australiensis*	12	Assemb. 1	Assemb. 1 & 2	Australia; New Caledonia
			Diaphanosoma unguiculatum	1	Assemb. 1	Assemb. 1	Australia; New Caledonia
			Latonopsis australis	4	Assemb. 1	Assemb. 1	Global
			Latonopsis brehmi dedekkeri	13	Assemb. 2	Assemb. 2	New Caledonia
	Laevicaudata	Lynceidae	*Lynceus insularis*	5	Assemb. 2	Assemb. 2	New Caledonia
			Lynceus sp. A	10	Assemb. 1	Assemb. 1 & 2	Australia; New Caledonia
			Lynceus sp. B	2	Assemb. 3	Assemb. 3	New Caledonia
	Spinicaudata	Limnadidae	*Eulimnadia sp. A*	8	Assemb. 1	Assemb. 1	New Caledonia
Maxillopoda (Copepoda)	Calanoida	Centropagidae	*Boeckella sibleti*	2	Assemb. 2	Assemb. 2	New Caledonia
			Boeckella spinogibba	19	Assemb. 2	Assemb. 2	New Caledonia
			Boeckella sp. A	1	Assemb. 4	Assemb. 4	New Caledonia
			Boeckella sp. B	1	Assemb. 2	Assemb. 2	New Caledonia
			Boeckella sp. C	2	Assemb. 3	Assemb. 3	New Caledonia

The bipartite species-sample network had 94 nodes (24 species and 70 samples) and 132 links. The infomap algorithm determined two hierarchical levels of clustering in the network. The first level distinguished the network in four clusters. Each cluster is considered as an assemblage hereafter (fig. 3). The second level delineated 15 sub-clusters with an average species richness of 1.6. Given this low species richness at the second level, we chose to focus exclusively on the first level (tab. S4).

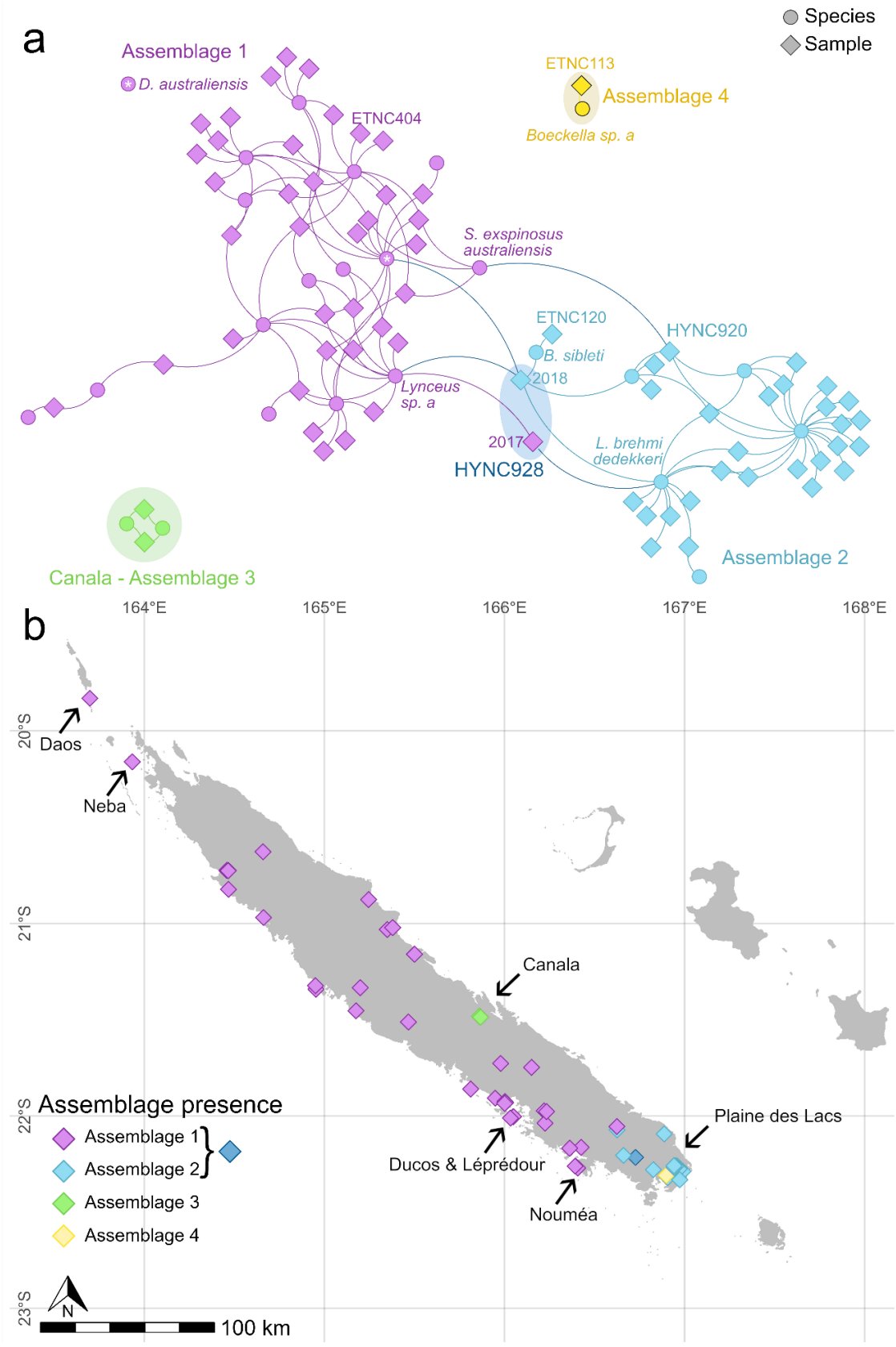

Figure 3 - Species-sample network coloured with each assemblage delineated by the clustering algorithm at the first level. Intermediate location HYNC928 is associated with both assemblages and is highlighted in dark blue. Isolated assemblages 3 and 4 are highlighted in green and yellow respectively (a). Presence map of each assemblage delineated by the clustering algorithm (b).

At the first level, two major clusters were delineated (assemblage 1 and 2 on fig. 3 and tab. 1). Assemblage 1 was composed of 15 species in 38 samples and occurred in most of Grande Terre, Ducos, Léprédour, Neba and Daos islands. Assemblage 2 was composed of 6 species in 29 samples and occurred in the southernmost area of Grande Terre, in and around the Plaine des Lacs. The two assemblages were mostly separated geographically (fig. 3b). The HYNC928 location was the only exception to this geographic separation as the clustering algorithm associated two assemblages (1 and 2) to this location sampled in 2017 and 2018. This location is highlighted by a blue oval on fig. 3a.

The two assemblages were related by four links between the 2018 sample of HYNC928 and species *Diaphanosoma australiensis* and *Lynceus sp. A*; between the 2017 sample of HYNC928 and species *Latonopsis brehmi dedekkeri*; and between HYNC920 and species *Simocephalus exspinosus australiensis*. The three species were the only ones found in samples affiliated with several assemblages and were all associated with assemblage 1 by the clustering algorithm (tab. 1).

Assemblage 3, highlighted in green on fig. 3a, was composed of two species (*Lynceus sp. B* and *Boeckella sp. C*) in two samples and assemblage 4, highlighted in yellow on fig. 3a, of one species (*Boeckella sp. A*) in one sample. Despite being relatively geographically close to other locations (fig. 3b), both assemblages are completely isolated and disconnected from any other part of the network (assemblage 3 and 4 on fig. 3a). As for assemblage 2, assemblages 3 and 4 were located on ultramafic massifs.

Sampling completeness and diversity estimates

Sampling completeness and diversity estimates are meaningful when sufficient samples are provided. As assemblages 3 and 4 were based on only two and one sample respectively, we computed the estimators only for assemblages 1 and 2. For both assemblages, sampling completeness increased with diversity order, highlighting undetected diversity especially for rare species (tab. 2). However, most frequent species were seemingly detected in assemblages 1 and 2 (fig. 4).

Hill numbers estimated a higher diversity in assemblage 1 for each diversity order. However, assemblage 2 appeared to have a higher proportion of rare species when comparing estimates at q = 0 with q = 1 and q = 2 (63.8-75.3% of estimated infrequent species for assemblage 2 and 40.9-49.9% for assemblage 1; tab. 2).

Table 2 - Sampling completeness and Hill numbers diversity estimates at three q orders.

Assemblage	Diversity order	Sampling Completeness	Observed diversity	Estimated diversity	Undetected species	% of undetected species
1	q = 0; all species	67.2%	D0 = 16	$\widehat{D0} = 23.79$	7.79	32.7%
	q = 1; frequent species	95.1%	D1 = 12.24	$\widehat{D1} = 14.04$	1.79	12.8%
	q = 2; super-frequent species	99.6%	D2 = 10.63	$\widehat{D2} = 11.92$	1.29	10.8%
2	q = 0; all species	53.8%	D0 = 9	$\widehat{D0} = 16.72$	7.72	46.2%
	q = 1; frequent species	91.4%	D1 = 5.25	$\widehat{D1} = 6.22$	0.96	15.5%
	q = 2; super-frequent species	99.6%	D2 = 3.92	$\widehat{D2} = 4.14$	0.22	5.3%

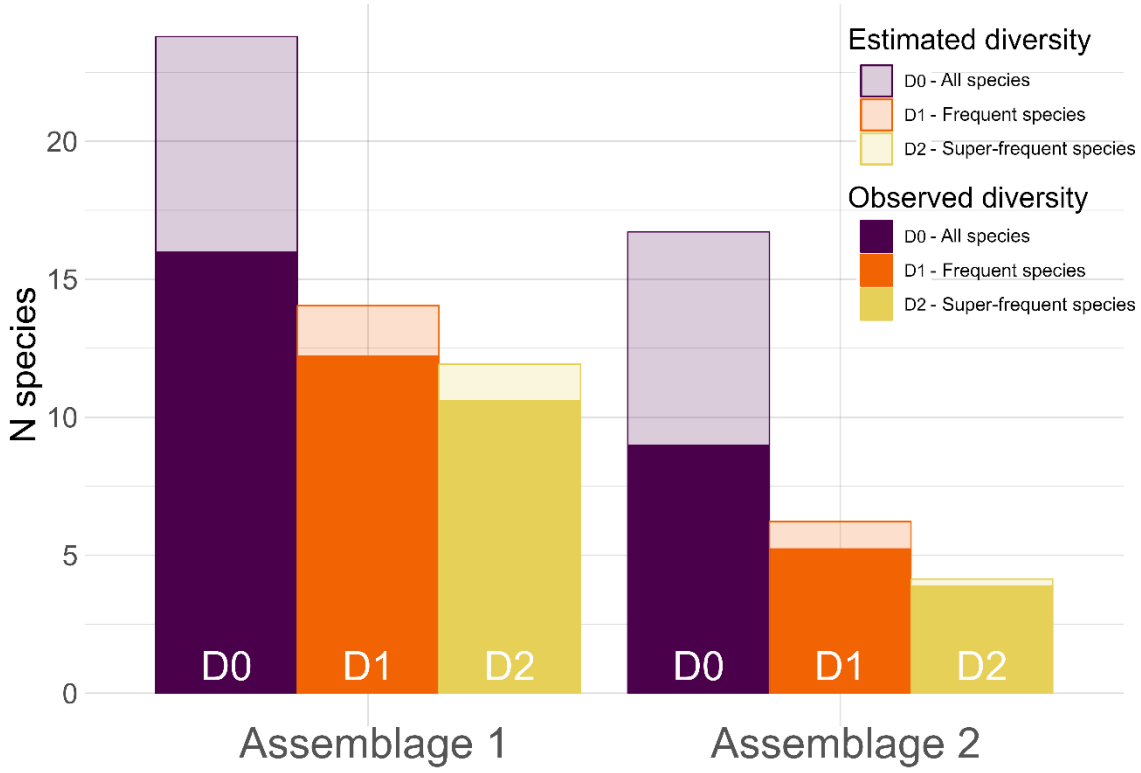

Figure 4 – Observed and estimated diversity at three q orders.

Assemblage distribution modelling

The full model computed on all four variables (ultramafic massifs, annual precipitations, sampling density and distance to freshwater) determined low variable importance for sampling density and distance to freshwater (supplementary data S2). Hence, we computed two other models, one with two variables, ultramafic massifs, and annual precipitations and one with three variables, sampling bias, ultramafic massifs, and annual precipitations. This last model with three variables showed the highest evaluation metrics (supplementary data S2) and was the least complex with most consensual and smooth responses curves (fig. 5a, b).

According to this last model, assemblage 1 is more likely to be observed in the absence of ultramafic massifs and at lower annual precipitation rates (highest suitability between 1000 and 1500 kg/m²/y), little variations are observed on response curves for sampling density (fig. 5a). Assemblage 2 is more likely to be observed in the presence of ultramafic soils and at higher annual precipitation rates (highest suitability between 2250 and 3340 kg/m²/y), this assemblage responded with higher suitability around 0.4 kernel density from our sampling (fig. 5b).

Assemblage 1 appears to be the most suitable assemblage across the majority of the archipelago, except for the southernmost region of Grande Terre, where assemblage 2 is observed with a higher suitability (fig. 5c). Figure 5c depicts the most suitability assemblage in terms of colour overlaid by its suitability represented in black of varying opacity. The lower the suitability of the most suitable assemblage, the higher the opacity of the black. In other words, the less it is possible to see which assemblage is most suitable on the map, the less it is probable to actually observe this assemblage in the area. Indeed, areas with the lowest suitability are situated predominantly at frontiers between both assemblages. Additionally, the majority of the area where assemblage 2 is most suitable has a relatively low suitability.

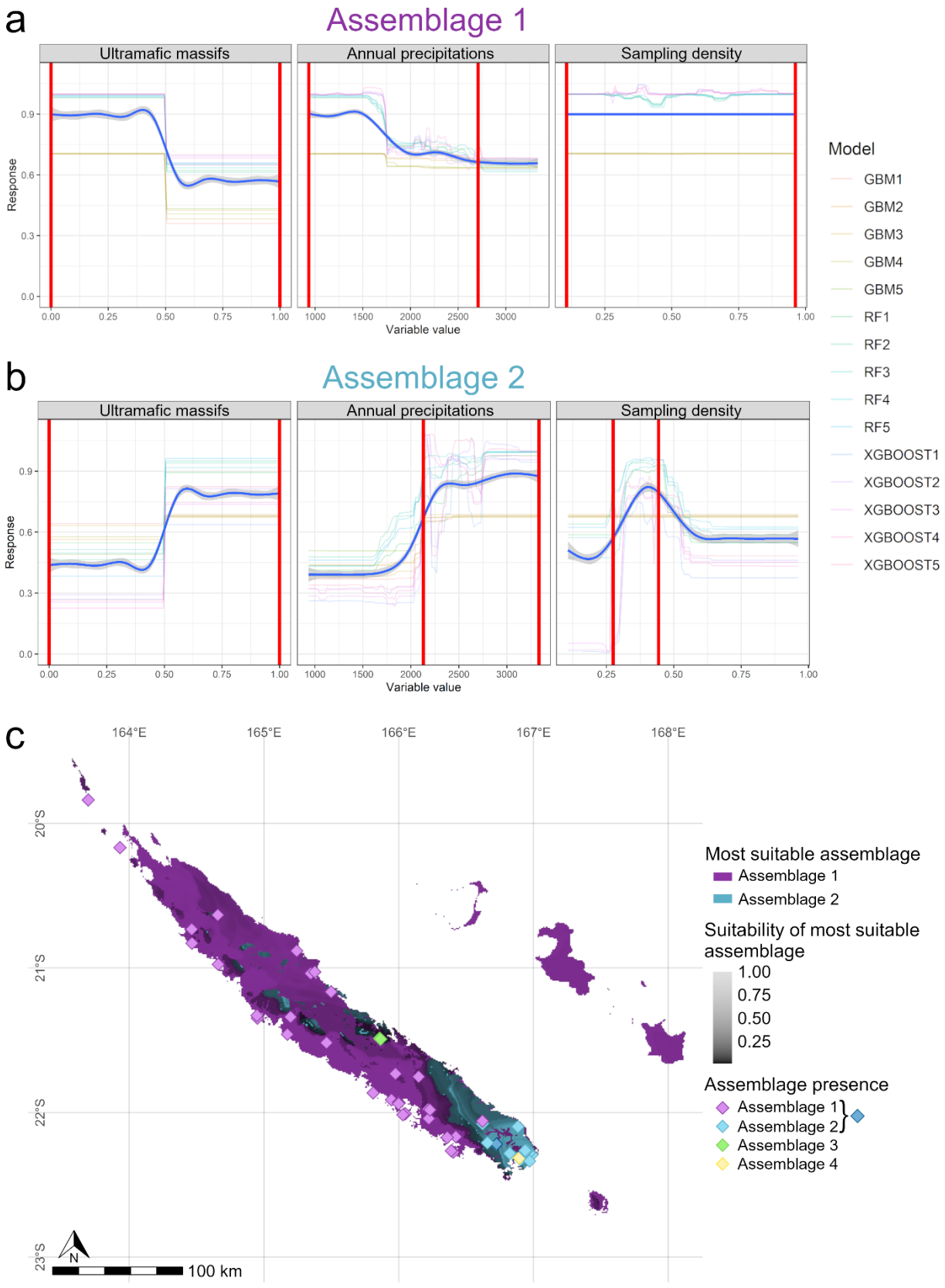

Figure 5 - Models' response plots of assemblages 1 and 2 for each selected variable. Variable ranges for observed presences of assemblages are represented by vertical red lines (a, b). Binary map of most suitable assemblage at each pixel (in purple and blue) overlaid by the mean suitability of the most suitable assemblage in black of varying opacity (c).

Discussion

Effects of ultramafic massifs and precipitations

The delineated assemblages and computed models demonstrated that the distribution of lentic freshwater crustacean assemblages seems to be primarily driven by the presence or absence of ultramafic soils and, to a lesser extent, by annual precipitation. Furthermore, the incorporation of sampling bias from our study permitted us to correct the response inconsistencies between models.

Links between ultramafic soils and the floral, fungal and microbial diversity in New Caledonia has been extensively studied (Amir et al., 2023; Gourmelon et al., 2016; Isnard et al., 2016; Isnard & Jaffré, 2024; Pillon et al., 2021). For example, a difference in pollinator composition has been demonstrated between ultramafic and non-ultramafic environments of the archipelago (Zakardjian et al., 2023). Numerous faunal taxa on the archipelago are known to be exclusively observed from ultramafic soils (Berman & Andersen, 2012; Hrivniak et al., 2023; Hudel et al., 2020; Keith, 2002; Nattier et al., 2013). However, no formal demonstration of this phenomenon using analytical tools has been made prior to this study.

Adaptations of plants to the high heavy metal concentrations in ultramafic soils are well known (*e. g.* mycorrhiza, accumulation organs). In lentic ecosystems, the effects of heavy metal are studied but mostly as a stressor (Faghihinia et al., 2021). In New Caledonia, the concentration of heavy metals is not the result of anthropogenic pollution but is naturally present in the environment since over 25 Mya (Chevillotte et al., 2006; Maurizot & Campbell, 2020). All species associated with assemblage 2 are, to present knowledge, endemic to New Caledonia while only one species associated with assemblage 1 is endemic to the archipelago. Higher proportion of endemic species on ultramafic massifs is also found in plants, pollinators and grasshoppers on the archipelago (Isnard et al., 2016; Isnard & Jaffré, 2024; Nattier et al., 2013; Zakardjian et al., 2023). The difference in heavy metal concentration itself can suffice as a factor for adaptative speciation that could explain the distinction between the two assemblages. However, more indirect effects could also explain the observed differences between ultramafic and non-ultramafic environments. Indeed, ultramafic and non-ultramafic environments are very different. Ultramafic environments appear to have lower fertility rates, lower species richness and higher habitat heterogeneity (Isnard et al., 2016; Morat et al., 2012; Pillon et al., 2021). Similarly, lentic environments on ultramafic soils show low primary productivity and low species richness (Bargier et al., 2018) which could notably lower the frequency of terrestrial and aerial macrofauna visits and consequently dispersion opportunities (Herteux et al., 2019).

The appearing preference of assemblage 1 for lower precipitation rates could indicate species functioning in ponds with shorter habitat duration. On average, without distinction between shared socioeconomic pathways and general circulation model, higher precipitation rates are predicted on the archipelago at both 2041-2070 and 2071-2100 horizons (CHELSA). It could indicate a wider spread of assemblage 2 in future decades. However, as assemblage 2 seems to be ultramafic obligate, a new potentially non-native assemblage might colonise the archipelago as well.

Diversity within assemblages

As with observed diversity, estimated total diversity is higher in assemblage 1 but there is a higher proportion of rare species in assemblage 2 that is exclusively located on ultramafic massifs (tab. 2). Regarding assemblage 1, it is notable that, except one potential endemic species, all species associated with it are also reported in Australia (Korovchinsky, 1981; Smirnov & Timms, 1983; Timms, 2015). In this context, a comparable assemblage could be identified in Australia which would deepen the knowledge on these assemblages and the links between Australia and New Caledonia biodiversity. Should a comparable assemblage be observed in Australia, it may be of interest to investigate the diversity levels there and ascertain whether the island biogeography assumption that richness is lower on isolated islands is verified within such assemblages (Whittaker et al., 2023).

Only three of the 24 total species were found in samples from both assemblages which implies these assemblages exhibit notable divergence from one another. Additionally, the two assemblages are geographically well separated in the archipelago. Assemblage 1 comprises more than half of the network nodes and is distributed over almost two-thirds of New Caledonia while assemblage 2 is distributed over a significantly smaller area (fig. 3, 5). In assemblages 1 and 2, the sampling appears to be incomplete especially for rare species. Nevertheless, frequent species are adequately sampled which is the most crucial to delineate assemblages.

We notice in the assemblages delineation that species classified as belonging to assemblage 1 were sometimes observed in samples from assemblage 2 and never the other way around. Assemblage 2 could comprise only specialists to ultramafic environments, which would preclude them from successfully colonising locations in non-ultramafic environments as observed for most ultramafic plant species in New Caledonia (Isnard et al., 2016). The species observed in both assemblages would be generalists. However, these species have only been sparsely observed in samples classified in assemblage 2, which is not consistent for truly generalist species.

The HYNC928 location sampled in 2017 and 2018 (highlighted in dark blue on fig. 3a), appears to be intermediate as species from both assemblages are observed in equilibrated proportions with one species of each assemblage in 2017 and two species of each assemblage in 2018. The sample from 2018 contains a fifth species, *Boeckella sibleti*, that is associated with assemblage 2. However, we observed this species in only one other sample, ETNC120 sampled in 2020. ETNC120 is also associated with assemblage 2 and *B. sibleti* is the only species we observed in the sample. Consequently, the affiliation of *B. sibleti* with assemblage 1 or 2 seems ambiguous which implies the affiliation of ETNC120 to assemblage 2 is ambiguous as well.

Considering this ambiguous belonging of locations HYNC928 and ETNC120 and species *B. sibleti* to assemblage 1 or 2, a buffer area or environmental gradient may exist where the species from the two assemblages can coexist to a limited extent. This hypothesis is further supported by the low suitability for both assemblages predicted by our models at the borders between these assemblages (fig. 5c). Such gradient between ultramafic and non-ultramafic environments has been posited for plant assemblages (Enright et al., 2001). Indeed, on ultramafic massifs of the archipelago, three major vegetal formations are found; low-altitude maquis (< 1000 m), high-altitude maquis (> 1000 m), and dense forests (Jaffre, 1996). Low-altitude maquis would be related with most locations associated with assemblage 2. Only one pond has been sampled in high-altitude maquis in Pic Ningua (ETNC401) where a single species has been identified, *Moina micrura*, this pond has been classified in assemblage 2. Interestingly, the intermediate locations HYNC928 and ETNC120 are both found in ultramafic dense forest assemblages, and both are located in areas where the models predict low suitability for the two assemblages.

Despite the impossibility to model their potential distribution, assemblages 3 and 4 are both present on ultramafic massifs which could indicate that they represent inadequately sampled sub-assemblages of assemblage 2. Ultramafic massifs show high complexity and heterogeneity (Chevillotte et al., 2006; Isnard et al., 2016; Nattier et al., 2013) which could explain sub-divisions of the assemblage in these environments. Regarding assemblage 4, such hypothesis seems relevant as it is located in an area where assemblage 2 is highly suitable. However, regarding assemblage 3, it is notable that the suitability of assemblages 1 and 2 are both low in the area. Indeed, locations associated with assemblage 3 are present on low-precipitations ultramafic massifs which are differing with conditions apparently preferred by assemblages 1 and 2.

Conservation

Ponds disappear at accelerating rates which is sufficient to be alarming (Haase et al., 2023; Markovic et al., 2017; Reid et al., 2019; Rhazi et al., 2012). Additionally, knowledge about their biota is scarce in tropical environments such as New Caledonia which could indicate an even worth situation in these areas as demonstrated for tropical vascular plants (Faghihinia et al., 2021; Junk, 2002; Vamosi & Vamosi, 2008).

Among the families included in this analysis (*i.e.*, Streptocephalidae, Triopsidae, Daphniidae, Macrothricidae, Moinidae, Sididae, Lynceidae, Limnadidae, Centropagidae), only two species

signalled in New Caledonia have not been sampled in this study, the Centropagidae *Dussartopages fagesi* (Dussart, 1986) and, the Daphniidae *Daphnia carinata mirabilis* (Stingelin, 1915). However, at least seven undetected species were estimated in each assemblage by the interpolation and extrapolation method. This estimation is indicative and insufficient to conclude for the exact number of unknown species on the archipelago. However, it is clear that most of the global microcrustacean biodiversity is unknown and New Caledonia should be no exception (Macedo et al., 2024).

Future predictions indicate wetter conditions that are potentially detrimental for assemblage 1. However, it is widespread on the archipelago and might also be present in Australia. Large distribution is an advantageous factor regarding extinction risks (McKinney, 1997; Terborgh & Winter, 1980). Assemblage 2 seems to face higher extinction risks with its lower species richness and narrower observed distribution. Additionally, the apparent preference of assemblage 2 for ultramafic massifs makes it face an immediate threat that is mining activity (Pascal et al., 2008).

In this study, known species are associated with one or several assemblages with distinctive features. In the field, the identification of several species from a particular assemblage could now be used to infer threats faced by the studied environment and apply effective conservation strategies. Models based on similar methods as the ones presented in this article have demonstrated their impact on conservation policies and applications on the field (Guisan et al., 2013).

Limitations and perspectives

The sampling is a major limitation in this study for several reasons. The first three years of sampling were exploratory as the location of many ponds were unknown. Despite methodical identification of interest locations on satellite images before the sampling, many ponds of small size are undetectable with this method and were sampled opportunistically. Additionally, some locations have been visited several times but the vast majority has only one sample. Unfortunately, many of the sampled ponds are difficult to access and, if temporary, might be dry most of the year which makes sampling unpredictable to some extent.

As highlighted in the introduction, temporary lentic freshwaters are dynamic systems. Indeed, depending on the length and periodicity of the hydroperiod, assemblages in these environments will be very different. Precipitations undoubtedly have a major impact on hydroperiods. However, many other factors such as soil granulometry, surrounding vegetation, connection to phreatic zones, air humidity and sun exposure affects the hydroperiod from local to regional scales. Consequently, models presented in this study seemingly lack one of the most important factor structuring communities that is hydroperiod. Knowing the exact hydroperiod of a pond requires daily surveillance of the location through direct observation or field sensors which would be a major enhancement in the presented models.

The incorporation of sampling density as an independent variable in the models is not the most satisfying way of dealing with sampling bias. However, as the variable importance computed by the models for sampling density was the lowest for both assemblages, its impact on projections seemed reasonably low. Additionally, the projected potential distribution of each assemblages seemed biologically coherent with our observations and with what has been posited for other taxa on the archipelago. Nevertheless, it would be of interest to try other bias correction techniques such as environmental filtering or the draw of background points to compare model performance and projections (Barber et al., 2022; Leroy, 2022; Varela et al., 2014).

Similarly, there are many methods for community distribution models. Ensemble models as used in this study have been deeply reviewed in the last decade and many methodological choices are required (Araújo et al., 2019; Franklin & Miller, 2010; Valavi et al., 2021). Many of these choices are hard to standardise and no consensus on best decision practice exists for the large majority of them (Feng et al., 2019; Leroy, 2022).

The lack of knowledge or the complexity of identification of several crustacean species living in the studied environment led the assemblages to be inferred from a largely filtered set of taxonomic groups among crustaceans. Indeed, a large portion of the diversity in our samples is represented

by Chydoridae and Ostracod species and adding these taxa to the analysis would be a future amelioration to make.

Ideally, models computed in our study should be validated with an independent sampling campaign. In addition, future studies on temporary freshwater communities in New Caledonia should probably focus on areas where the models predict low suitability for the two assemblages. Such studies would help clarify whether these regions constitute different assemblages or buffer areas.

Appendices

Table S1 - Sampled locations sorted in full.

Sample single identifier	Longitude (x)	Latitude (y)	Sampling date(s)	Other names given to the location
HYNC4114	166.42577	-22.16381	17-06-2018	
HYNC4014	165.49944	-21.15934	07-06-2018	
HYNC4000	166.22052	-21.97417	04-06-2018	
HYNC918	166.95902	-22.26997	16-06-2018	HYNC4101
ETNC006	164.95308	-21.3421	15-04-2021	Pindai mare temporaire
HYNC920	166.9521	-22.26282	05-06-2018	HYNC4005
HYNC4111	166.95397	-22.26296	16-06-2018 12-06-2020	Doline croissante
HYNC4066	165.17555	-21.45432	13-06-2018	
HYNC4102	166.94141	-22.25926	16-06-2018 17-05-2022	
HYNC4109	166.95335	-22.26197	16-06-2018	
HYNC2608	165.86094	-21.48206	09-04-2018	
HYNC909	164.659	-20.628	17-11-2016	
ETNC110	166.99156	-22.28856	03-06-2020	DT41; DP41
ETNC109	166.95919	-22.25989	08-06-2020	DP46
HYNC2604	165.867	-21.48756	09-04-2018	
HYNC925	166.95259	-22.26107	16-06-2018 12-06-2020	HYNC4107; Lac en long
HYNC4110	166.95346	-22.26281	16-06-2018	
ETNC117	166.952	-22.26239	05-06-2020	
HYNC928	166.72775	-22.21552	25-03-2017 05-06-2018	HYNC4004
ETNC002	166.04828	-22.00455	14-01-2021	Ducos mare 1
ETNC107	166.96889	-22.27547	09-06-2020	DP13
ETNC120	166.62531	-22.07308	23-06-2020	Pourina; PPRB
HYNC4104	166.94773	-22.26835	16-06-2018	
ETNC116	166.90658	-22.32086	22-06-2020	DOL_11
ETNC113	166.89847	-22.30944	05-06-2020	DT70
HYNC4112	166.36215	-22.16813	17-06-2018	
HYNC2741	165.94847	-21.90796	08-12-2017	
HYNC2703	166.00233	-21.92528	07-12-2017	
ETNC004	166.05052	-22.00462	14-01-2021	Ducos mare 3
HYNC4098	166.82705	-22.27972	16-06-2018	
HYNC927	166.95324	-22.2621	16-06-2018	HYNC4108
HYNC4105	166.94776	-22.26257	16-06-2018	
ETNC008	164.94987	-21.3238	15-05-2021	Pindai mare temporaire 2
HYNC931	166.94835	-22.25917	16-06-2018 05-06-2020	HYNC4106; DT53
ETNC001	166.03328	-22.01154	14-01-2021	Mare aux canards
HYNC4003	166.22512	-22.03785	04-06-2018	
HYNC4060	165.19906	-21.33434	13-06-2018	
HYNC4079	164.45752	-20.72473	14-06-2018	
HYNC4012	165.50048	-21.16028	07-06-2018	
HYNC4008	166.39332	-22.26009	06-06-2018	
HYNC4075	164.46567	-20.7248	14-06-2018	
ETNC112	166.96989	-22.27567	09-06-2020	DT45; DP45
ETNC124	166.97336	-22.33189	26-06-2020	DP60
HYNC924	166.95164	-22.26234	05-06-2020	DT20
HYNC4009	166.40684	-22.27068	06-06-2018	
HYNC4055	164.66218	-20.96972	12-06-2018	
HYNC2747	166.00635	-21.93062	08-12-2017	
HYNC4084	164.46736	-20.8234	14-06-2018	
HYNC2802	165.46647	-21.51258	22-11-2017	HYNC1802
HYNC2672	165.81242	-21.86069	04-12-2017	
HYNC4103	166.94166	-22.26875	16-06-2018	
ETNC302	166.8873	-22.09387	19-05-2022	Unia02

ETNC310	166.66102	-22.20532	18-05-202	Doline mare Valentin
HYNC4019	165.34887	-21.03231	08-06-2018	
HYNC4002	166.23357	-21.97767	04-06-2018	
ETNC209	163.69716	-19.83093	24-04-2022	Belep09
HYNC4006	166.39224	-22.26134	06-06-2018	
HYNC4020	165.37911	-21.02222	08-06-2018	
ETNC401	166.15042	-21.74806	23-04-2023	Pic ningua
ETNC016	165.97887	-21.72764	22-02-2021	Mont do
HYNC2699	166.00122	-21.93533	05-12-2017	
HYNC4074	164.46548	-20.72657	14-06-2018	
HYNC4024	165.24526	-20.87638	08-06-2018	
ETNC404	166.62423	-22.05538	22-04-2023	Haute pourina nord
ETNC406	163.93282	-20.16094	01-04-2023	ABC_002

Data S2 - Inputs and outputs for data cleaning, analyses and evaluation as described in the "Workflow_Royaux2026.pdf" file.
https://doi.org/10.5281/zenodo.18837988

Data S3 - ODMAP protocol. "ODMAP_Royaux2026_2025-09-01.csv"
https://doi.org/10.5281/zenodo.18837988

Table S4 - Species-cluster associations as computed by the network clustering algorithm at the second level.

Class	Family	*Species*	Associated cluster
Branchiopoda	Streptocephalidae	*Streptocephalus archerii*	Cluster 1
	Triopsidae	*Triops longicaudatus intermedius*	Cluster 1
	Daphniidae	*Simocephalus exspinosus australiensis*	Cluster 3
		Simocephalus acutirostratus	Cluster 1
		Ceriodaphnia rigaudi	Cluster 4
		Daphnia cephalata	Cluster 1
		Daphnia longicephala	Cluster 6
	Macrothricidae	*Macrothrix sp. A*	Cluster 11
		Macrothrix triserialis	Cluster 7
		Macrothrix spinosa	Cluster 2
	Moinidae	*Moina micrura*	Cluster 5
	Sididae	*Diaphanosoma unguiculatum*	Cluster 6
		Diaphanosoma australiensis	Cluster 3
		Latonopsis brehmi dedekkeri	Cluster 9
		Latonopsis australis	Cluster 2
	Lynceidae	*Lynceus insularis*	Cluster 8
		Lynceus sp. A	Cluster 1
		Lynceus sp. B	Cluster 14
	Limnadidae	*Eulimnadia sp. A*	Cluster 1
Maxillopoda (Copepoda)	Centropagidae	*Boeckella spinogibba*	Cluster 8
		Boeckella sibleti	Cluster 10
		Boeckella sp. A	Cluster 15
		Boeckella sp. B	Cluster 13
		Boeckella sp. C	Cluster 14

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Author contributions (CRediT)

Conceptualization: R.C., L.B., LB.Y., R.N.; Methodology: R.C., L.B.; Software: R.C., L.B.; Validation: R.C., L.B.; Formal analysis: R.C.; Investigation: R.C., M.N., C.N., R.N.; Resources: M.N., C.N., R.N.; Data Curation: R.C.; Writing - Original Draft: R.C.; Writing - Review & Editing: L.B., M.N., C.N., LB.Y., R.N.; Visualization: R.C.; Supervision: LB.Y., R.N.; Project administration: C.R.; R.N.; Funding acquisition: R.N.

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Conflict of interest disclosure

The authors declare that they comply with the PCI rule of having no financial conflicts of interest in relation to the content of the article.

Data, scripts, code, and supplementary information availability

Raw data are available online: https://doi.org/10.48579/PRO/CD4FC4.

Scripts and code are available online: https://github.com/ColineRoyaux/DM and https://github.com/ColineRoyaux/cleanSIG

Supplementary data are available online: https://doi.org/10.5281/zenodo.18837988

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