

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

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Introduction

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

53 A large proportion of ponds worldwide undergo cyclic drying which has profoundly structuring
54 influence on the biota. The persistence of populations in temporary ponds implies necessary
55 drought survival traits, such as diapausing eggs (Brock et al., 2003; Incagnone et al., 2015;
56 Williams, 2006). Furthermore, the habitat duration, also called hydroperiod, is a crucial factor
57 influencing populations and communities inhabiting temporary ponds (Olmo et al., 2016; Schneider
58 & Frost, 1996; Tavernini, 2008). For instance, a species that attains maturity 13 days after the
59 pond is flooded such as *Lynceus bififormis* would not be observed in a temporary pond with a 10-
60 day hydroperiod (Wang et al., 2014). As modelled by Macedo et al., (2024), many micro-
61 crustacean species inhabiting ponds are not described, especially in temporary waters. Such
62 Linnean shortfall in continental micro-crustacean induces the six other shortfalls described by
63 Hortal et al., (2015), highlighting the depth of our current knowledge gaps regarding these
64 organisms. In New Caledonia, most species of micro-crustaceans are known from less than 6
65 locations, and in many cases, just a single one (Longhurst, 1955; Olesen et al., 2016; Timms,
66 1985).

67 Communities of crustacean species in ponds are highly reliant on all aforementioned variables
68 of the environment (Feld et al., 2016). In this article, we describe crustacean species assemblage
69 which is defined as a multi-specific group of taxonomically related populations that occur in a given
70 space (Stroud et al., 2015). In New Caledonia, lentic freshwater crustacean assemblages are
71 notably composed of e.g., the endemic longtail tadpole shrimp sub-species *Triops longicaudatus*
72 *intermedius* (Longhurst, 1955), of the recently described copepod *Boeckella sibleti* (Royaux et al.,
73 2024), of the globally distributed Ostracoda species *Candonocypris novaezelandiae* (Martens et
74 al., 2019), and of the remarkable Australian-New Caledonian water flea *Daphnia longicephala*
75 (Timms, 1985). Lentic freshwater micro-crustaceans have never been studied from the perspective
76 of species assemblages on the archipelago.

77 Nouvelle-Calédonie (New Caledonia, Kanaky) is an archipelago located in the southwest
78 Pacific Ocean. Its main island, Grande Terre, is continental and separated from Australia
79 approximately 105 Mya (Maurizot & Campbell, 2020). The archipelago is known for its outstanding
80 biodiversity and has one of the highest proportions of endemic species on earth (Veron et al.,
81 2019). In New Caledonia, mean annual precipitation rates exhibit a considerable range over the
82 territory, from 887 to 3339 mm, which results to markedly disparate conditions in the numerous
83 permanent and temporary ponds that are distributed over the archipelago. The density of lentic
84 freshwaters is notably high in the extreme south of Grande Terre in the Plaine des Lacs and the
85 Parc Provincial de la Rivière Bleue, which has been designated a “wetland of international
86 importance” under the Ramsar Convention (Jeanpert et al., 2016). This area is also notable for its
87 heavy metal-rich soils, which originate from the alteration of ultramafic massifs. Such massifs cover
88 approximately one-third of the archipelago and are considered as a significant factor in
89 environmental filtering there (Isnard & Jaffré, 2024; Zakardjian et al., 2023). Indeed, a significant
90 proportion of endemic species of the archipelago are known to be exclusively found in ultramafic
91 environments (Nattier et al., 2013; Pillon et al., 2021). However, the high concentrations of notably
92 nickel, cobalt, and chromium in ultramafic rocks and soils are an important economic resource for
93 the archipelago. The mining activity on ultramafic massifs is present in Grande Terre and

94 surrounding islands since the 19th century, which has many impacts on landscapes and
95 ecosystems (Boula et al., 2022; Germande et al., 2022; Pascal et al., 2008). Freshwaters are
96 particularly sensitive to mining and other anthropogenic perturbations, which have led them to be
97 considered among the most vulnerable environments in terms of biodiversity (García-Girón et al.,
98 2023; Tickner et al., 2020). Indeed, in New Caledonia, many ponds are notably found in and around
99 mining facilities, the largest being the Prony Resources mine in the Plaine des Lacs. This facility
100 extracts nickel from soils with a rather low heavy metal concentration. The process inevitably
101 produces many chemical residuals which pollutes freshwaters (Germande et al., 2022). In addition
102 to evident impact through the excavation of soils, it creates inert wastes in the form of fine dust
103 that is filling local freshwaters (Boula et al., 2022). Beside mining activity, the agricultural practice
104 and frequent wildfires caused the plant cover to be considered “modified” for 40% of the territory
105 (Isnard & Jaffré, 2024). The modification of plant covers inevitably has heavy impacts on the
106 distribution and characteristics of freshwaters (Reid et al., 2019; Stocker et al., 2023). These
107 threats are particularly significant for pond micro-crustaceans inhabiting freshwater islands on dry
108 oceans they cannot cross on their own (Incagnone et al., 2015).

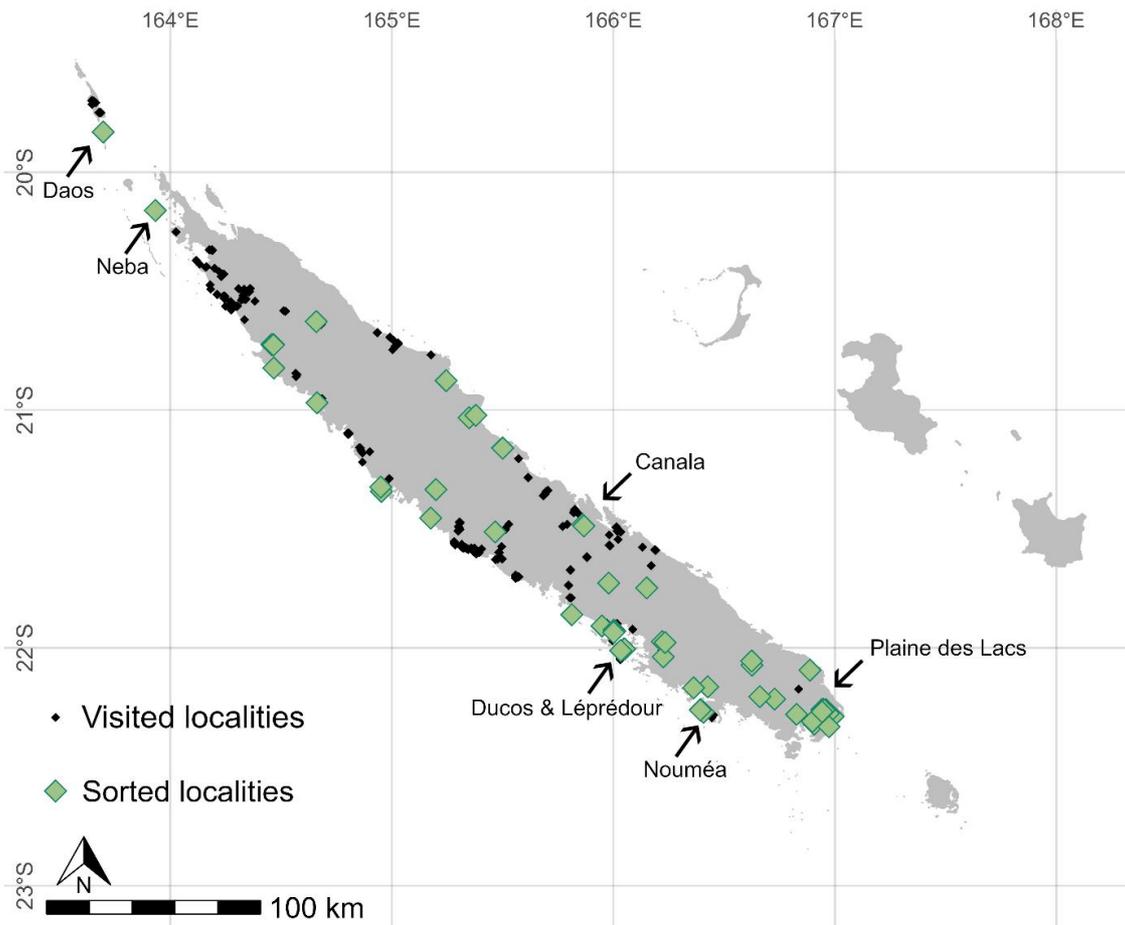
109 Based on 70 samples of crustaceans from freshwater ponds on the archipelago, we provide
110 new records of species that were unknown in New Caledonia, contributing to decrease the
111 Wallacean knowledge shortfall (*i.e.*, gaps in the known geographic distribution of species; Hortal
112 et al., 2015).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

120 Material and methods

121 Sampling and identification

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

129 In total, 70 samples were collected from the 65 locations and we entirely sorted their content
130 to identify the species of crustaceans (fig. 1; supplementary tab. S1). We based identifications
131 under binocular microscope (and optical microscope when required) on keys by El-moor Loureiro
132 (1997), Korovchinsky (2001), Quinlan & Bayly (2017), Smirnov & Timms (1983), Stingelin (1915),
133 and Timms (1985). We pooled all individuals of the same species and from the same sample in
134 clean 80-90% ethanol in a glass tube with a screw cap and identification were verified by 2-3
135 different persons.



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Figure 1 - Visited and sorted localities.

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Assemblage delineation

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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.

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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, MapEquation will uncover a hierarchical clustering

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

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

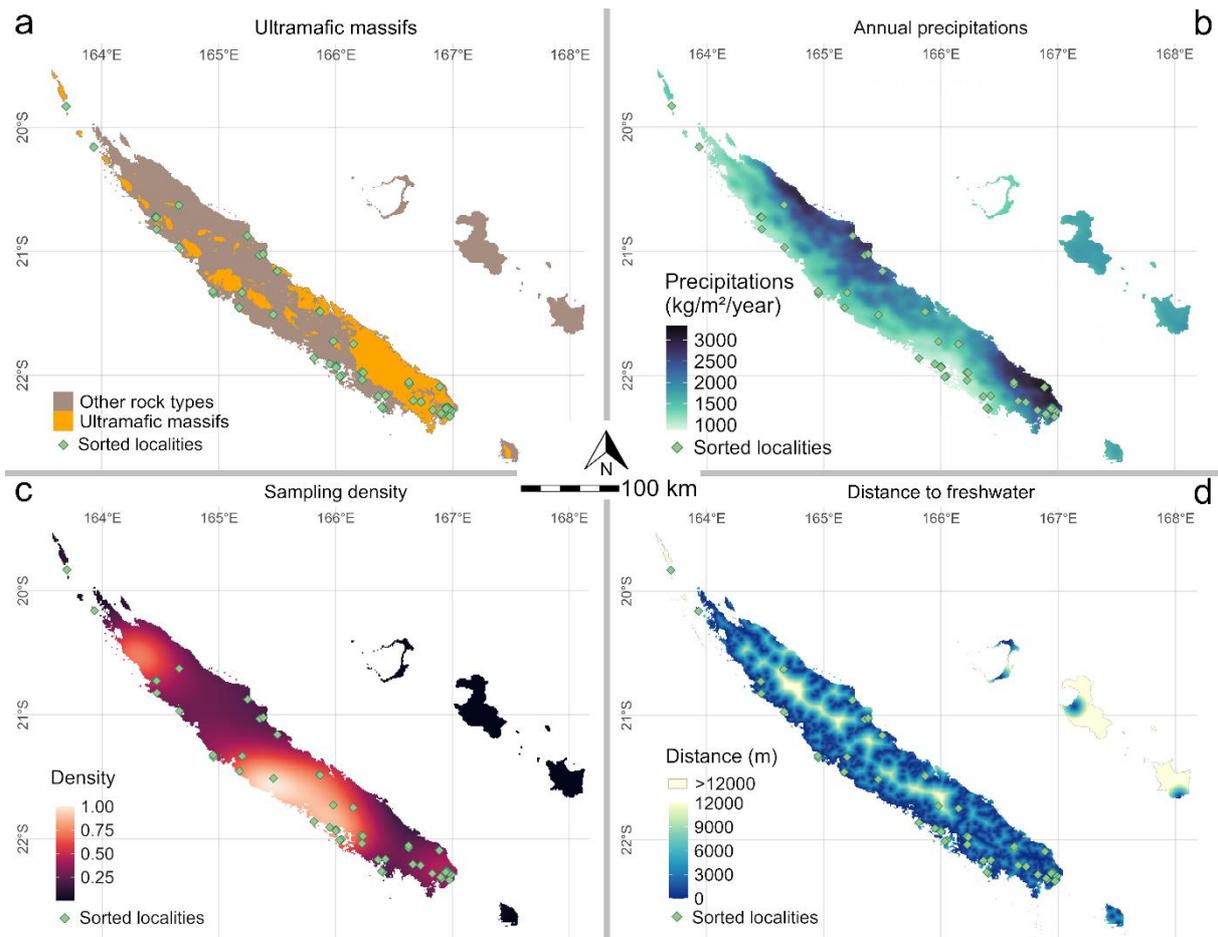
170 **Sampling completeness and diversity estimates**

171 For each assemblage delineated with the bipartite network, we computed sampling
172 completeness and diversity estimates using the interpolation and extrapolation for three
173 dimensions of biodiversity method based on Hill numbers (Chao et al., 2020; M. O. Hill, 1973;
174 Ramiro-Sánchez et al., 2023). Hill numbers characterise the diversity of species with equal
175 frequencies depending on the q parameter and, although typically computed on abundance data,
176 they can also be computed on occurrence data as this is the case here. Hence, each order $q = 0$,
177 $q = 1$, and $q = 2$ corresponds to the estimation of the total species richness, the number of frequent
178 species and the number of highly frequent species respectively (see Chao et al., 2020). We
179 computed estimates of Hill numbers at the three orders on the whole dataset and on delimitations
180 based on the previously delineated assemblages using the R 4.2.2 packages iNEXT.3D 1.0.4 and
181 iNEXT.4steps 1.0.0 (Chao & Hu, 2024). Sampling completeness estimation is critical to validate
182 the delineated assemblages and identify lacks in the dataset. Estimated Hill numbers permit us to
183 better comprehend each delineated assemblage and compare their characteristics.

184 **Assemblage distribution modelling**

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

200 We retrieved spatial data layers for the presence of ultramafic massifs (fig. 2a; peridotite v23-
201 09-2021; [https://georep-dtsi-sgt.opendata.arcgis.com/datasets/dtsi-sgt::massifs-de-
202 p%C3%A9ridotites-au-50-000-2](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,
203 <https://chelsa-climate.org/bioclim/>) and the distance to freshwater based on the global maximum
204 water extent (fig. 2d; 1984-2021, European Commission, [https://global-surface-
205 water.appspot.com/](https://global-surface-water.appspot.com/); Pekel et al., 2016) on online open data repositories. In addition, we computed
206 the sampling density (kernel) of all campaigns with R 4.2.2 package MASS 7.3-58.1 (fig. 2c).



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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).

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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.

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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).

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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.

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233 We applied the ODMAP protocol to reproducibly report our modelling protocol (Zurell et al.,
 234 2020). It is available in supplementary material (supplementary data S3). The complete analytical
 235 workflow from data preparation and assemblage delineation to final assemblage distribution
 236 models is available in supplementary data S2 along with associated data. Scripts are available on
 237 Github (<https://github.com/ColineRoyaux/BioCommunity>;
 238 <https://github.com/ColineRoyaux/cleanSIG>; <https://github.com/ColineRoyaux/DM>).

239 **Results**

240 **Identification and assemblage delineation**

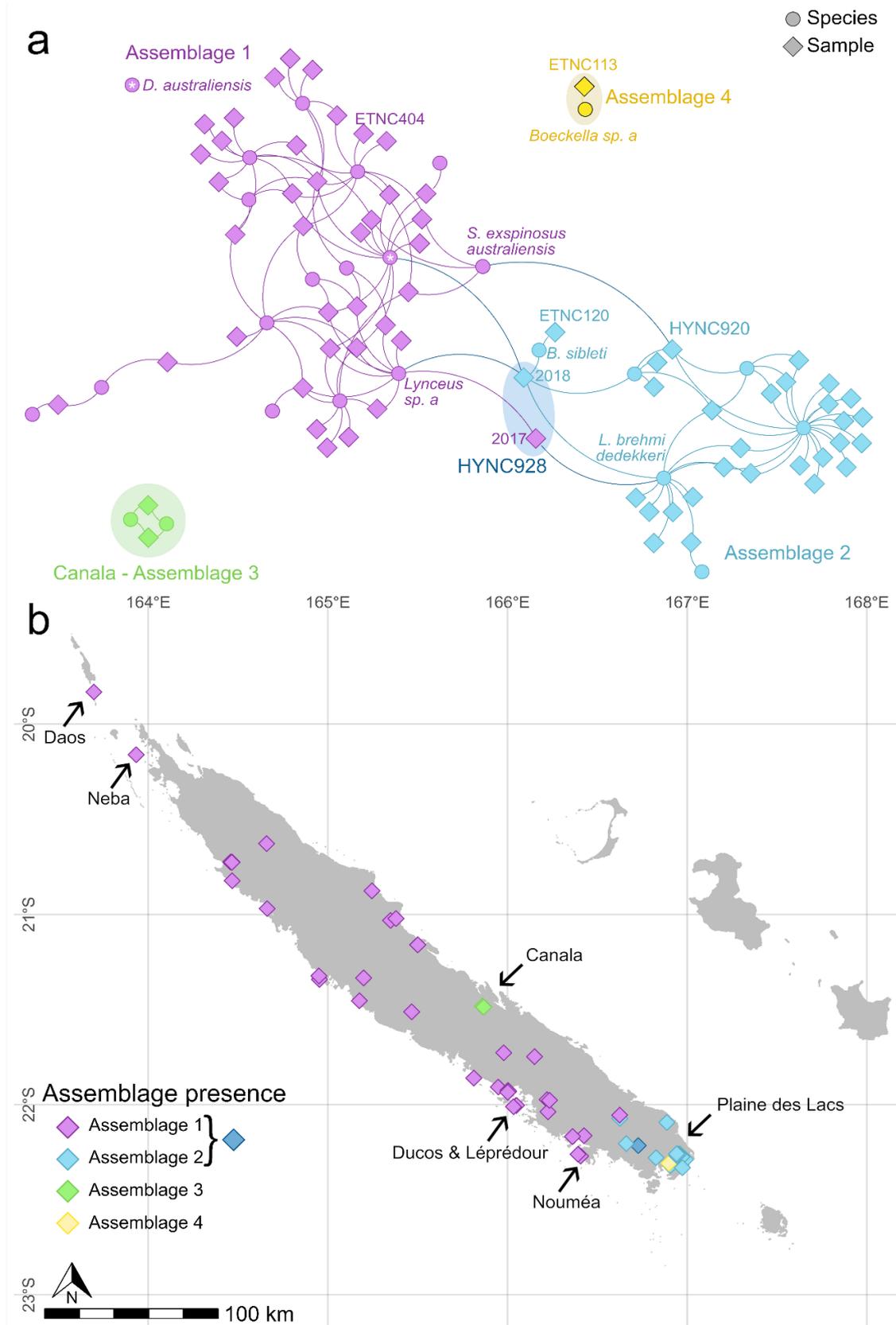
241 In total, we identified 24 species of 13 genera in the 70 samples (tab. 1). The highest species
 242 richness was found in HYNC4002 with 6 species detected and most locations had a species
 243 richness of 1 (n=32) or 2 (n=17).

244 **Table 1** - Species identified in sorted samples, their occurrence count, assemblage
 245 associated with them using the network clustering algorithm, the assemblages
 246 associated with the samples in which they were observed and their known
 247 distribution.

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

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249 The bipartite species-sample network had 94 nodes (24 species and 70 samples) and 132
250 links. The infomap algorithm determined two hierarchical levels of clustering in the network. The
251 first level distinguished the network in four clusters. Each cluster is considered as an assemblage
252 hereafter (fig. 3). The second level delineated 15 sub-clusters with an average species richness of
253 1.6. Given this low species richness at the second level, we chose to focus exclusively on the first
254 level (tab. S4).



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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).

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

269 The two assemblages were related by four links between the 2018 sample of HYNC928 and
 270 species *Diaphanosoma australiensis* and *Lynceus sp. A*; between the 2017 sample of HYNC928
 271 and species *Latonopsis brehmi dedekkeri*; and between HYNC920 and species *Simocephalus*
 272 *exspinosus australiensis*. The three species were the only ones found in samples affiliated with
 273 several assemblages and were all associated with assemblage 1 by the clustering algorithm (tab.
 274 1).

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

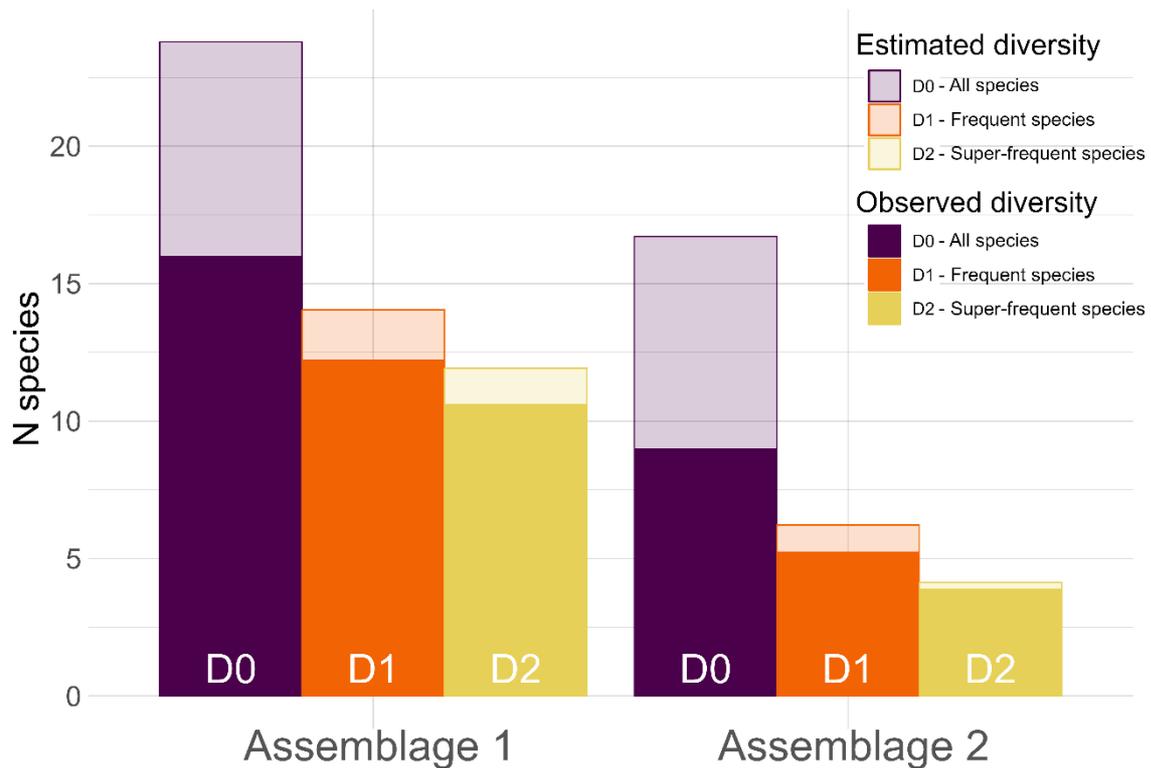
281 **Sampling completeness and diversity estimates**

282 Sampling completeness and diversity estimates are meaningful when sufficient samples are
 283 provided. As assemblages 3 and 4 were based on only two and one sample respectively, we
 284 computed the estimators only for assemblages 1 and 2. For both assemblages, sampling
 285 completeness increased with diversity order, highlighting undetected diversity especially for rare
 286 species (tab. 2). However, most frequent species were seemingly detected in assemblages 1 and
 287 2 (fig. 4).

288 Hill numbers estimated a higher diversity in assemblage 1 for each diversity order. However,
 289 assemblage 2 appeared to have a higher proportion of rare species when comparing estimates at
 290 $q = 0$ with $q = 1$ and $q = 2$ (63.8-75.3% of estimated infrequent species for assemblage 2 and 40.9-
 291 49.9% for assemblage 1; tab. 2).

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

Assemblage	Diversity order	Sampling Completeness	Observed diversity	Estimated diversity	Undetected species	% of undetected species
1	$q = 0$; all species	67.2%	$D_0 = 16$	$\widehat{D}_0 = 23.79$	7.79	32.7%
	$q = 1$; frequent species	95.1%	$D_1 = 12.24$	$\widehat{D}_1 = 14.04$	1.79	12.8%
	$q = 2$; super-frequent species	99.6%	$D_2 = 10.63$	$\widehat{D}_2 = 11.92$	1.29	10.8%
2	$q = 0$; all species	53.8%	$D_0 = 9$	$\widehat{D}_0 = 16.72$	7.72	46.2%
	$q = 1$; frequent species	91.4%	$D_1 = 5.25$	$\widehat{D}_1 = 6.22$	0.96	15.5%
	$q = 2$; super-frequent species	99.6%	$D_2 = 3.92$	$\widehat{D}_2 = 4.14$	0.22	5.3%



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

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Assemblage distribution modelling

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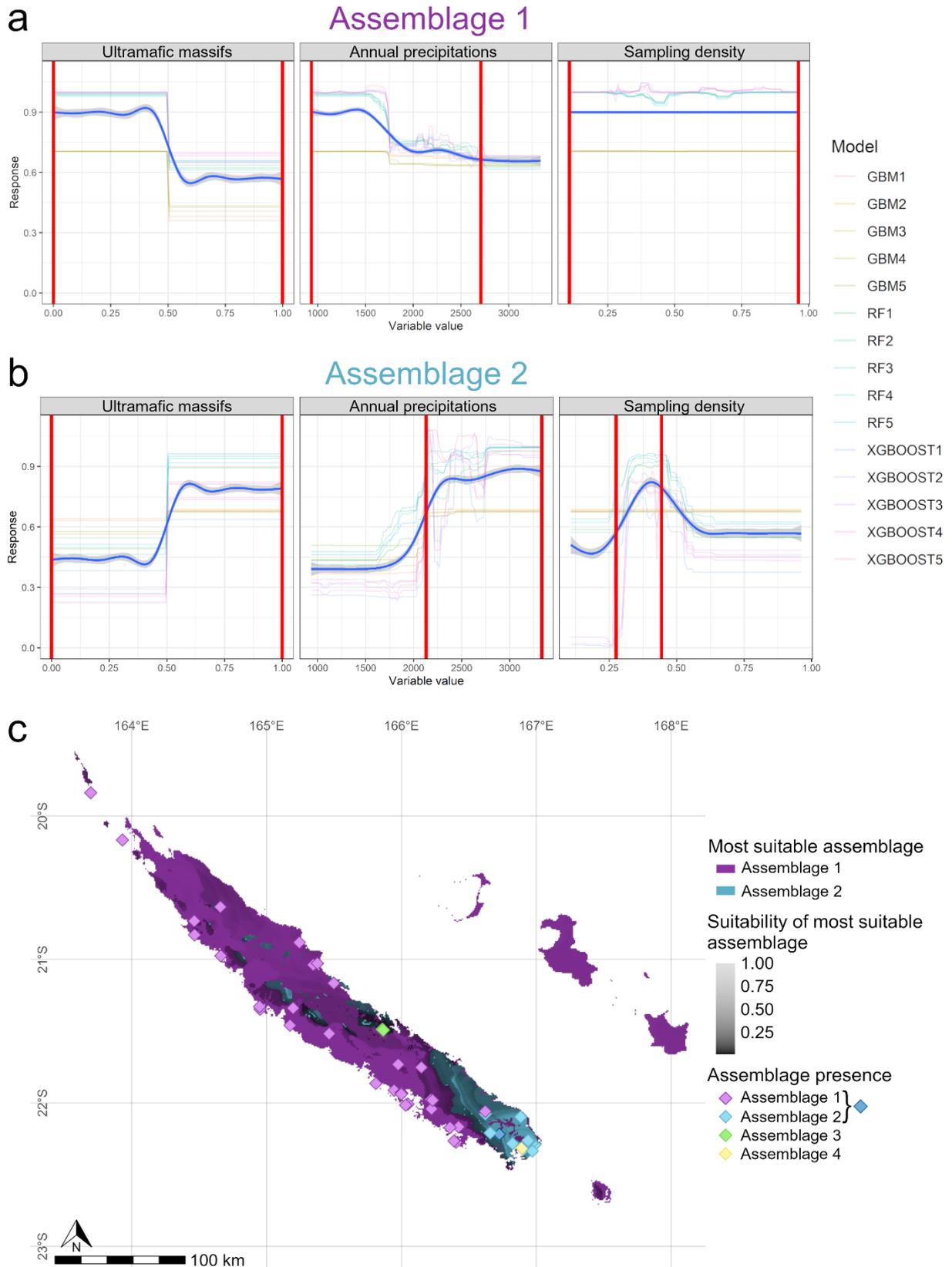
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The full model computed on all four variables (ultramafic massifs, annual precipitations, sampling density and distance to freshwater) determined low variable importance for sampling density and distance to freshwater (supplementary data S2). Hence, 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.



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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).

325

Discussion

326 **Effects of ultramafic massifs and precipitations**

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

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

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

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

364 **Diversity within assemblages**

365 As with observed diversity, estimated total diversity is higher in assemblage 1 but there is a
366 higher proportion of rare species in assemblage 2 that is exclusively located on ultramafic massifs
367 (tab. 2). Regarding assemblage 1, it is notable that, except one potential endemic species, all
368 species associated with it are also reported in Australia (Korovchinsky, 1981; Smirnov & Timms,
369 1983; Timms, 2015). In this context, a comparable assemblage could be identified in Australia
370 which would deepen the knowledge on these assemblages and the links between Australia and
371 New Caledonia biodiversity. Should a comparable assemblage be observed in Australia, it may be
372 of interest to investigate the diversity levels there and ascertain whether the island biogeography
373 assumption that richness is lower on isolated islands is verified within such assemblages
374 (Whittaker et al., 2023).

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

382 We notice in the assemblages delineation that species classified as belonging to assemblage
383 1 were sometimes observed in samples from assemblage 2 and never the other way around.
384 Assemblage 2 could comprise only specialists to ultramafic environments, which would preclude
385 them from successfully colonising locations in non-ultramafic environments as observed for most
386 ultramafic plant species in New Caledonia (Isnard et al., 2016). The species observed in both
387 assemblages would be generalists. However, these species have only been sparsely observed in
388 samples classified in assemblage 2, which is not consistent for truly generalist species.

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

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

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

419 Conservation

420 Ponds disappear at accelerating rates which is sufficient to be alarming (Haase et al., 2023;
421 Markovic et al., 2017; Reid et al., 2019; Rhazi et al., 2012). Additionally, knowledge about their
422 biota is scarce in tropical environments such as New Caledonia which could indicate an even worth
423 situation in these areas as demonstrated for tropical vascular plants (Faghihinia et al., 2021; Junk,
424 2002; Vamosi & Vamosi, 2008).

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

427 signalled in New Caledonia have not been sampled in this study, the Centropagidae
428 *Dussartopages fagesi* (Dussart, 1986) and, the Daphniidae *Daphnia carinata mirabilis* (Stingelin,
429 1915). However, at least seven undetected species were estimated in each assemblage by the
430 interpolation and extrapolation method. This estimation is indicative and insufficient to conclude
431 for the exact number of unknown species on the archipelago. However, it is clear that most of the
432 global microcrustacean biodiversity is unknown and New Caledonia should be no exception
433 (Macedo et al., 2024).

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

440 In this study, known species are associated with one or several assemblages with distinctive
441 features. In the field, the identification of several species from a particular assemblage could now
442 be used to infer threats faced by the studied environment and apply effective conservation
443 strategies. Models based on similar methods as the ones presented in this article have
444 demonstrated their impact on conservation policies and applications on the field (Guisan et al.,
445 2013).

446 **Limitations and perspectives**

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

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

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

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

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

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

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

486

Appendices

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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

488 **Data S2** - Inputs and outputs for data cleaning, analyses and evaluation as
 489 described in the “Workflow_Royaux2026.pdf” file.
 490 <https://doi.org/10.5281/zenodo.18837988>

491 **Data S3** - ODMAP protocol. “ODMAP_Royaux2026_2025-09-01.csv”
 492 <https://doi.org/10.5281/zenodo.18837988>

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

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

495 Acknowledgements

496 The New Caledonia Hydrobiological expeditions 2016–2018 were conducted under the ‘La
 497 Planète Revisitée’ programme implemented by the Muséum national d’Histoire naturelle (MNHN),
 498 Paris, in partnership with the Conservatoire d’Espaces naturels (CEN). We deeply thank Pascale
 499 Joannot, head of the expeditions programme at MNHN, and Phillippe Bouchet, the expedition
 500 leader. These expeditions were operated under permits issued by New Caledonia’s Province Sud
 501 (under APA_NCPS_2017_028) and Province Nord, and the organizers thank Emmanuel Coutures
 502 and Isabelle Jurquet (Province Sud) and Jean-Jérôme Cassan and Yannick Monlouis (Province
 503 Nord) for their help in obtaining these permits. We also thank Sébastien Faninoz and Alice Leblond.

504 Authors thank Lucie Lenglet, Tancrède Bourgeois, Gabrielle Ourous, Félix Navarro, Angel Arnold
505 and Agathe Moulin for their participation in the pre-processing of the samples.
506 Finally, authors dedicate this work to Loyola Até 'Fanfan'.

507 Author contributions (CRediT)

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

513 Funding

514 Funding for 'La Planète Revisitée' expeditions were provided by the Gouvernement de la
515 Nouvelle-Calédonie, Province Sud, Province Nord, Office des Postes et Télécommunications
516 (OPT), Maison de la Nouvelle-Calédonie, and the Ministère Français des Outre-mer. Funding for
517 'Vies d'Ô douce' expeditions were provided by call for projects ATM (Actions Transversale du
518 Muséum) from the Muséum national d'Histoire naturelle, by the Appels A Projets (AAP) SUD and
519 the AAP transverse axe MIDI (Migration, Dispersion des organismes aquatiques) from UMR
520 BOREA (Unité Mixte de Recherche Biologie des Organismes et Ecosystèmes Aquatiques).

521 Conflict of interest disclosure

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

524 Data, scripts, code, and supplementary information availability

525 Raw data are available online: [URL in progress] for full raw dataset, meanwhile all intermediary
526 outputs with filtered data and sampling density are available in Appendix S2].
527 Scripts and code are available online: <https://github.com/ColineRoyaux/DM> and
528 <https://github.com/ColineRoyaux/cleanSIG>
529 Supplementary data are available online: <https://doi.org/10.5281/zenodo.18837988>

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