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1 **Local and regional controls of phylogenetic structure at the high-latitude range limits**
2 **of corals**

3

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16 Key words: range limit, phylogenetic structure, niche conservatism, environmental filtering, coral,
17 trait

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21

22 **Abstract**

23

24 Understanding how range edge populations will respond to climate change is an urgent research
25 priority. Here we used a phylogenetic community ecology approach to examine how ecological and
26 evolutionary processes shape biodiversity patterns of scleractinian corals at their high-latitude range
27 limits in eastern Australia. We estimated phylogenetic signal in seven ecologically important
28 functional traits and conducted tests of phylogenetic structure at local and regional scales using the
29 net relatedness (NRI) and nearest taxon indices (NTI) for presence/absence and abundance data.
30 Regional tests showed light phylogenetic clustering, indicating that coral species found in this
31 subtropical-to-temperate transition zone are more closely related to each other than are species on
32 the nearby, more northerly Great Barrier Reef. Local tests revealed variable patterns of
33 phylogenetic clustering and overdispersion and higher than expected phylogenetic turnover among
34 sites. In combination, these results are broadly consistent with the hierarchical filtering model,
35 whereby species pass through a regional climatic filter based on their tolerances for marginal
36 conditions and subsequently segregate into local assemblages according to the relative strength of
37 habitat filtering and species interactions. Conservatism of tested traits suggests that corals will
38 likely track their niches with climate change. Nevertheless, high turnover of lineages among sites
39 indicates that range shifts will probably vary among species and highlights the vulnerability and
40 conservation significance of high-latitude reefs.

41

42

43 INTRODUCTION

44

45 Understanding local and regional controls on biodiversity is fundamental to understanding species
46 range dynamics and how they may be affected by global change. Ecological community structure
47 arises from a combination of processes that operate at different spatial and temporal scales. Species
48 may occur in the same communities by occupying different niches (i.e. limiting similarity) and / or
49 because they have specialised traits that allow them to persist locally (i.e. environmental filtering)
50 [1]. Classical ecological theory predicts that the relative importance of these processes in driving
51 biodiversity patterns varies systematically along stress-gradients, with abiotic factors predominant
52 at high elevation, high latitude, and other abiotically stressful regions, and biotic interactions
53 relatively more important in abiotically more benign regions [2, 3]. Moreover, a growing body of
54 literature suggests that biotic and abiotic filters operate at different spatial scales, with
55 environmental conditions often found to be the dominant process at regional scales and biotic
56 interactions relatively more important at local scales [4, 5]. Quantifying the relative strength of
57 these processes at multiple spatial scales is necessary to accurately predict species range shifts in
58 response to climate change [3]. For instance, when biotic interactions are important in setting
59 species range limits, models solely based on climatic influences could overestimate species range
60 shifts in response to climate change [3].

61

62 Phylogenies are increasingly used to investigate ecological and evolutionary drivers of biodiversity
63 patterns. The central idea is that patterns of phylogenetic community structure differ depending on
64 whether environmental filtering or competition is the dominant assembly process [6]. This is based
65 on the premise that closely related species have similar traits [i.e. trait conservatism; 7] and
66 consequently require similar environmental conditions and resources to persist. Close relatives
67 therefore compete more intensely for the same resources, which is thought to limit coexistence and
68 to drive trait and niche difference [2]. Environmental filtering, on the other hand, can prevent

69 species with unsuitable traits from occurring locally. Under classical ecological theory, competition
70 is therefore generally expected to limit the similarity of co-occurring species, leading to
71 phylogenetic overdispersion, while environmental filtering is thought to drive the co-occurrence of
72 closely related species, leading to phylogenetic clustering [6]. For example, seminal work by
73 Cavender-Bares et al. [8] found that co-occurring oak trees in Florida were phylogenetically
74 overdispersed, suggesting that competition restricts close relatives from inhabiting the same areas.
75 Recent advances in coexistence theory challenge the universality of this pattern, highlighting that
76 competition can also lead to the co-occurrence of similar species, if the traits in question are
77 associated with competitive dominance [9].

78
79 Gradients in phylogenetic alpha and beta diversity and tests for phylogenetic structure have been
80 used to infer the dominant assembly processes operating in local and regional assemblages [6]. This
81 work indicates that biotic and abiotic filters often operate at different spatial scales, such that local
82 assemblages are embedded in regional assemblages and species sequentially pass through historical,
83 abiotic and biotic filters [4, 10]. For example, regional climate might initially filter species with
84 certain traits (e.g. cold tolerance) into large patches of homogeneous habitat (e.g. alpine mountains)
85 that are further partitioned at finer scales (e.g. soil type). Species then segregate into local
86 assemblages based on the relative strength of habitat filtering versus competition [4, 6]. These
87 processes can be detected by spatially nesting analyses [6] and by combining metrics of
88 phylogenetic alpha and beta diversity [4]. For example, environmental filtering at local scales
89 combined with high turnover of habitat types in the region is expected to manifest in local
90 phylogenetic clustering and high phylogenetic beta diversity among sites [4].

91
92 While studies of phylogenetic community ecology are well established in terrestrial ecosystems,
93 this approach is underrepresented in marine ecosystems [reviewed in 11, but see 12, 13]. Due to
94 their ecological diversity, eco-morphological plasticity and habitat sensitivity, scleractinian corals

95 are especially suited to examining the role of evolutionary history in shaping extant communities. In
96 eastern Australia, diverse coral assemblages extend into high latitudes (32°48'S) south of the Great
97 Barrier Reef [14-16], where various coral species occur at the edges of their ranges and experience
98 cooler, darker and more seasonal and variable conditions than their tropical counterparts [17]. These
99 high-latitude reefs represent ideal systems in which to investigate how evolutionary stability of
100 species traits and phylogenetic relatedness may influence biodiversity patterns in marginal and
101 changing environments. A recent study found that these range-edge coral assemblages are shaped
102 by trait-mediated environmental filtering, with similar species co-occurring in the region [15] along
103 strong environmental gradients [17]. As phylogenetic relatedness does not predict species'
104 ecological similarity *per se* [18], investigating the evolutionary stability of ecological traits in these
105 physiologically challenging environments is a critical next step in predicting species responses to
106 climate change. For instance, if species' climatic tolerances are stable over time (i.e. conserved),
107 they will probably only expand their ranges to environments that are similar to their core ranges,
108 and be constrained in their evolutionary responses to novel environmental conditions [7].

109

110 In this study, we take a hierarchical approach (Fig. 1) to disentangle the relative importance of
111 regional to local processes in generating biodiversity patterns of corals in the subtropical-to-
112 temperate transition zone (26°36'S to 32°48'S) along the eastern Australian coast. To investigate
113 evolutionary stability of species traits, we initially estimate phylogenetic signal in ecologically
114 important functional traits. Under niche conservatism we expect closely related species to be more
115 similar in their functional traits than distantly related species, implying that there has been limited
116 evolutionary change since species have diverged from a common ancestor [7]. We subsequently
117 combine analyses of phylogenetic alpha and beta diversity and of phylogenetic structure at multiple
118 spatial scales to evaluate how evolutionary and ecological processes shape the distribution of corals
119 in this biogeographic transition zone (Fig.1). To examine the shared history of high-latitude coral
120 assemblages with the Great Barrier Reef (GBR; situated to the north of the study region), we test

121 whether species found on eastern Australian high-latitude reefs are a random subset of the GBR
122 species pool in terms of their phylogenetic relatedness (Fig. 1A, B). Consistent with stronger
123 influence of environmental filtering at the high-latitude margins of species ranges [19], we expect
124 that the species within the high-latitude species pool are more closely related to one another than
125 are the species within the Great Barrier Reef species pool. We then perform site-level tests of
126 phylogenetic structure to investigate whether local assemblages are phylogenetically clustered or
127 overdispersed (Fig. 1C) and whether patterns vary with latitude. Due to increasingly marginal
128 environmental conditions for corals towards higher latitudes, we expect coral species to be more
129 closely related to each other at higher latitude sites and high turnover of lineages (i.e. high
130 phylogenetic beta diversity; Fig. 1C) among sites in this biogeographic transition zone.

131

132 **MATERIALS AND METHODS**

133

134 **Ecological data**

135

136 *Coral species abundances*

137 We determined species abundance distributions of scleractinian corals at 17 locations
138 (Supplementary Fig. S1) along a latitudinal gradient (26°36'S to 32°48'S) in the subtropical-to-
139 temperate transition zone in coastal eastern Australia [15]. We quantified percent cover of 85 coral
140 species from photographic belt transects using the random point count method [600 points per
141 transect, total of 51,000 points; see 15].

142

143 *Coral functional traits and phylogeny*

144 To examine functional strategies of corals, we characterised each species based on seven traits
145 known to influence the ecology of corals [20]. We included the three structural traits colony
146 morphology, corallite formation, and corallite size, as they undergo strong environmental filtering

147 at high-latitudes [15], as well as reproductive mode, sexual pattern, larval development rate and
148 symbiont transmission mode to characterise reproductive strategies [21-23]. Following Keith et al.
149 [24] egg size was used as a proxy for larval development rate, because small eggs develop more
150 rapidly [25]. The character states of all categorical traits were expressed as separate binary traits,
151 where ‘1’ indicates that the species displays the trait and ‘0’ that it does not. For example,
152 reproductive mode was classified as two separate binary traits: brooding and spawning (see
153 supplementary material for more information on traits). Due to the known variation with latitude in
154 other traits [e.g. growth rate; 26], and our inability to quantify this variation due to data deficiency,
155 we did not include more traits in our analyses. We used the coral ‘supertree’ of Huang and Roy [13]
156 to construct phylogenies of the 85 coral species recorded in our surveys and of the 412 species from
157 the GBR species pool obtained from the Atlas of Living Australia [27].

158

159 **Statistical analyses**

160

161 *Tests for phylogenetic signal in traits*

162 We tested for phylogenetic signal in traits using the D statistic [28] for binary traits (i.e. colony
163 morphology, corallite formation, reproductive mode, sexual pattern and symbiont transmission),
164 and Pagel’s λ [29] for the traits corallite size and larval development rate. Lower D values indicate
165 stronger phylogenetic signal (i.e. more conserved trait evolution), whereby a value of 0 equates to a
166 Brownian model (i.e. conserved trait evolution) and a value of 1 to random phylogenetic structure
167 (i.e. no signal). Negative D values indicate that traits are extremely clumped (i.e. more conserved
168 than under Brownian motion) and D values greater than 1 indicate phylogenetic overdispersion [28].
169 Conversely, higher values of Pagel’s λ indicate stronger phylogenetic signal, where λ equal to zero
170 means no phylogenetic signal and λ equal to 1 indicates trait evolution consistent with Brownian
171 motion. *P* values indicate departure from random phylogenetic structure and from Brownian
172 structure (i.e. non-significant *P* values for Brownian motion indicate conserved trait evolution).

173

174 *Patterns in phylogenetic diversity and tests for phylogenetic structure*

175 We quantified phylogenetic diversity patterns of corals using two metrics that are sensitive to
176 patterns at different depths of the phylogeny and identify processes operating at different
177 evolutionary time-scales [6], mean pairwise distance (MPD) and mean nearest taxon distance
178 (MNTD). MPD represents the average phylogenetic distance between all species in an assemblage
179 and is sensitive to tree-wide (i.e. more ancestral) patterns. MNTD represents the average distance
180 between each species and its closest relative and is thus sensitive to patterns at the tips of the
181 phylogeny (i.e. more recent events). In comparative analyses, MPD and MNTD values can be
182 affected by differences in species richness among sites. At our study sites, coral species richness
183 ranged between 52 and 2 species; we therefore standardised the observed MPD and MNTD values
184 with respect to expected values calculated under a null model that controls for coincidental
185 gradients in species richness. More specifically, we calculated the net relatedness index (NRI) and
186 the nearest taxon index (NTI) to test whether species in local assemblages were phylogenetically
187 clustered or overdispersed i.e. relatively more closely or distantly related than randomly expected,
188 respectively [6, 30]. We compared the observed MPD and MNTD values to null distributions
189 generated by shuffling the species names across the tips of the phylogeny (1000 times). This null
190 model randomises the relatedness of species to one another, but leaves the abundance distributions
191 and species richness of local assemblages unchanged. In addition to these site level tests, we also
192 conducted a regional test to determine whether coral species found in the subtropical-to-temperate
193 transition zone (i.e. all species that we recorded at the 17 study sites; Fig. 1B) are more closely or
194 distantly related than the species in the GBR phylogeny (Fig. 1A). For both local and regional tests,
195 positive NRI/NTI values indicate phylogenetic clustering while negative values indicate
196 phylogenetic overdispersion [30] (Fig. 1C). We performed nonparametric multidimensional scaling
197 ordination to visualise the relationships among patterns in phylogenetic structure, community-
198 weighted trait means, and coral community structure at the study sites.

199

200 Phylogenetic beta diversity was calculated in a way analogous to the NRI and NTI metrics, by
201 comparing the observed phylogenetic beta diversities to the patterns expected under a null model
202 that randomly shuffles the species names across the GBR phylogeny. Positive values of beta_NRI
203 and beta_NTI indicate higher than randomly expected phylogenetic turnover of species in pairs of
204 local assemblages; negative values indicate lower than expected phylogenetic turnover. As the coral
205 supertree contains a number of polytomies, we conducted all analyses for 1000 fully resolved trees
206 [13] and report results as the means over the 1000 trees. We calculated all metrics using both
207 presence/absence and abundance data, with respective results identified by the letters ‘pa’ and ‘ab’
208 (e.g. beta_NRIpa, beta_NRIab). When used with abundance data the interpretation of metrics
209 changes from phylogenetic distances among taxa to distances among individuals. We used
210 generalised additive models to evaluate the relationships between phylogenetic alpha diversity
211 metrics and latitude. We selected smoothness using restricted maximum likelihood and specified
212 smoothness with up to three effective degrees of freedom. We used Procrustes analysis to test the
213 association of phylogenetic beta diversity patterns and geographic distance (in degrees latitude) and
214 visualised site-level beta diversities using boxplots. All analyses were conducted using the packages
215 ‘picante’ [31], ‘caper’ [32], ‘vegan’ [33], and ‘mgcv’ [34] in R [35].

216

217 **RESULTS**

218

219 **Tests for phylogenetic signal in traits**

220

221 We found a phylogenetic signal for all tested functional traits, as their phylogenetic structures were
222 significantly different from random and not significantly different from Brownian motion (Table 1).
223 Indeed, six of the binary traits (sexual pattern, symbiont transmission, laminar growth, meandroid
224 corallites, encrusting-to-massive and branching-to-tabular growth) had negative D values,

225 indicating that they were more phylogenetically conserved than under a Brownian model [28].
226 Arborescent growth had the weakest signal and showed modest clumping (Table 1).

227

228 **Patterns in phylogenetic diversity and tests for phylogenetic structure**

229

230 Overall, the regional test for phylogenetic structure indicates that the coral species present on high-
231 latitude reefs (the high-latitude species pool) are more closely related to one another than are the
232 species in the GBR species pool. Phylogenetic structure for NRI (NRI = 0.842) and NTI (NTI =
233 1.289; Table S1 in supplementary material) was related to a clustering pattern, although values
234 calculated for 1000 phylogenetic trees were only significantly clustered for approximately 25% of
235 trees (third quartile: NRI = 1.193, NTI = 1.516). Site level tests of phylogenetic structure revealed
236 contrasting patterns for NRI and NTI, except for northern- and southernmost sites where both
237 metrics were positive (Fig. 2). Phylogenetic structure for most sites was clustered at the tips of the
238 phylogeny (NTI > 0) and overdispersed or close to random when measured at deep levels in the
239 phylogeny (NRI < 0), with NRI and NTI metrics generally showing both low positive and negative
240 values. NRI_{Ipa} showed a concave relationship with latitude ($R^2 = 0.549$, deviance explained = 60.5,
241 $p = 0.002$), but NRI_{Iab} ($R^2 = 0.162$, DE = 25.5, $p = 0.192$), NTI_{Ipa} ($R^2 = 0.006$, DE = 6.12, $p =$
242 0.356), and NTI_{Iab} ($R^2 = 0.028$, DE = 9.240, $p = 0.252$) were independent of latitude (Fig. 2).

243

244 Assemblages that showed basal and terminal clustering (red circles in Fig. 3) were characterised by
245 species with branching-to-tabular morphology, large corallites, fast development rates,
246 hermaphroditic sexual pattern, brooding reproduction, and vertical symbiont transmission (e.g.
247 *Pocillopora*, *Stylophora*, *Acanthastrea*). This pattern was seen across sites except at Black Rock,
248 which had high abundance of laminar species that were gonochoric broadcast spawners and
249 transmit their symbionts horizontally (e.g. *Turbinaria* spp.). Assemblages that showed contrasting
250 patterns for NRI and NTI (green diamonds and blue triangles in Fig. 3) generally showed large

251 variation in species traits, except for Flinders Reef (orange square in Fig. 3), which associated
252 strongly with arborescent morphology, spawning reproduction and horizontal symbiont
253 transmission (e.g. *Acropora* spp.). Note that vectors represent associations of community-weighted
254 trait means with the nMDS axes and that individual species don't necessarily possess the trait
255 combinations listed above.

256

257 Analyses of phylogenetic betadiversity showed that most sites showed higher than expected
258 phylogenetic turnover at both basal and terminal levels ($\beta\text{-NRI}$ and $\beta\text{-NTI} > 0$), and that this
259 pattern was stronger when abundance information was used (Fig. 4). With the exception of
260 $\beta\text{-NRIpa}$ (Procrustes correlation $t = 0.48$; $p = 0.015$), phylogenetic turnover patterns were
261 independent of geographic distance (Fig. 4). Indeed, some geographically close site pairs (within 0-
262 3 degrees latitude of each other) had high terminal phylogenetic beta diversity ($\beta\text{-NTIab}$),
263 indicating high turnover of abundant species from site to site (Fig. 4). $\beta\text{-NRIpa}$ and $\beta\text{-NTIpa}$
264 were positively correlated with each other (Procrustes correlation $t = 0.67$, $p = 0.001$), indicating
265 that site pairs with high basal turnover tended to also have high terminal turnover ($\beta\text{-NTI} > 0$).
266 This relationship was not significant ($t = 0.21$, $p = 0.929$) when species abundances were considered.

267

268 **DISCUSSION**

269

270 **Phylogenetic niche conservatism of corals**

271

272 Understanding species range dynamics and how they may be affected by global change requires the
273 consideration of multiple ecological and evolutionary processes [36]. Our results suggest that coral
274 species attenuate at higher latitudes in response to habitat filtering that is mediated by conserved
275 ecological niches. Niche conservatism has been invoked to explain large-scale biogeographic
276 gradients, such as the latitudinal diversity gradient [reviewed in 7]. This is based on the premise that

277 many groups originated in the tropics and are limited from colonising temperate regions by niche
278 conservatism (such as lack of adaptations to survive cold winter temperatures). Conversely, recent
279 studies have found multimodality of latitudinal gradients in species distributions and thermal
280 affinities of marine species [e.g. 37] and linked these patterns to adaptations of ‘bridge species’ at
281 the edges of the tropics and subsequent colonisation of temperate regions [i.e. the out of the tropics
282 hypothesis’; 38]. While rigorous tests of these hypotheses require data for entire species ranges, our
283 results indicate trait conservatism for corals at their high-latitude range limits and we find
284 phylogenetic diversity patterns that are consistent with species sorting in these marginal
285 environments. These findings are consistent with a recent study of habitat affinities of marine
286 invertebrates over geological time - niche conservatism was common in the oceans, but variable
287 among clades, with coral and sponges among the most conservative [39].

288

289 We found a phylogenetic signal in all tested species traits (Table 1). Larval development rate,
290 corallite size, sexual patterns and symbiont transmission showed the strongest conservatism among
291 the tested traits. Indeed, six of the binary traits (sexual pattern, symbiont transmission, laminar
292 growth, meandroid corallites, encrusting-to-massive and branching-to-tabular growth) were more
293 phylogenetically conserved than under a Brownian model [28]. Structural traits such as corallite
294 size and colony morphology undergo strong filtering in this region, whereby coral species with
295 similar trait expressions frequently co-occur at the same sites [15]. Corallite size has been linked
296 with energy storage and reproductive investment [40], and colony shape with light interception [41]
297 and it is plausible that these traits enhance energy acquisition [15] in these colder and light-limited
298 environments [17]. This is also consistent with the observation that corals on high-latitude reefs in
299 Australia and Japan share traits relevant to environmental tolerance [42].

300

301 Faster larval development rates and larger depth ranges were recently found to increase the
302 likelihood that coral species traverse faunal breaks [24]. Indeed, in our study species with relatively

303 fast development rates, including *Paragoniastrea australensis*, *Turbinaria* spp., *Acanthastrea* spp.
304 and *Pocillopora* spp., were abundant and widely distributed across the high latitude study region
305 [15]. Larval developmental time has important ecological implications for marine organisms
306 because it affects dispersal distance and connectivity [22, 25]. For instance, high relative abundance
307 of brooding corals, whose larvae are ready to settle upon release [25], is thought to be important for
308 population establishment and persistence on Lord Howe Island, the world's southernmost coral reef
309 [43, 44]. In our study, the strong association of brooding reproduction and fast development rates
310 with coral assemblages that were phylogenetically clustered (red circles in Fig. 3) also support the
311 hypothesis that the capacity to derive new recruits from local populations is important in these
312 marginal habitats [43].

313 314 **Phylogenetic community ecology of high-latitude coral assemblages**

315
316 Overall, regional tests revealed phylogenetic clustering of coral assemblages, indicating that coral
317 species on high-latitude reefs are on average more closely related with one another than are species
318 in the GBR species pool. While this is generally consistent with regional filtering, NRI and NTI
319 values only showed significant clustering for approximately 25% of the 1000 phylogenetic trees.
320 Site level results (Fig. 2) support the role of local filtering, indicating that patterns of phylogenetic
321 clustering and overdispersion vary among sites and at ancestral and more recent temporal scales.
322 This is consistent with other studies that found closely related or functionally similar species co-
323 occurring at larger spatial scales and more distantly related or dissimilar species co-occurring
324 locally. For example, local tree frog assemblages in the Americas were generally overdispersed,
325 while regional assemblages were frequently clustered in their body sizes [10]. Moreover, the
326 authors found that regional processes tend to be stronger in temperate than in tropical zones, such
327 that antagonistic regional and local filtering can substantially mask variation in trait dispersion [10].

328

329 We found that most assemblages contained species that were distributed randomly or slightly
330 overdispersed with respect to the entire tree ($NRI < 0$), but were clustered towards the tips of the
331 tree ($NTI > 0$). Thus, although local assemblages support numerous lineages that are widely spread
332 across the entire phylogeny, they harbour many close relatives within those lineages. Such evenness
333 in tree-wide phylogenetic structure (NRI) of local assemblages indicates that a diverse range of
334 lineages has been able to disperse to and establish on many high-latitude reefs, including many
335 species in the Acroporidae family that are the predominant reef builders on tropical coral reefs [45].
336 Nevertheless, the presence of close relatives within those lineages indicates the co-occurrence of
337 species with similar traits and tolerances for marginal conditions. Branch tips represent more recent
338 divergences, where new species have formed. Species that are closely related at the tips of the
339 phylogeny are therefore generally expected to occupy more similar niches and to have similar
340 resource needs when species traits are conserved [6]. The traits branching-to-tabular morphology,
341 large corallite sizes, hermaphroditic sexual pattern, brooding reproductive mode, fast development
342 rates, and vertical symbiont transmission were most strongly associated with phylogenetically
343 clustered assemblages (red circles in Fig. 3) that included *Pocillopora*, *Stylophora*, *Acanthastrea*
344 and *Micromussa* species. Moreover, gonochoric sexual pattern, broadcast spawning reproduction,
345 horizontal symbiont transmission and laminar growth also appear to be advantageous at sites that
346 were phylogenetically clustered (green diamonds in Fig. 3). In particular, these sites had high
347 abundance of several *Turbinaria* species that tend to do well in marginal environments [15, 46].

348

349 Contrary to our expectation, species at higher latitudes were not phylogenetically more related to
350 each other than those at lower latitudes. NRI_{pa} even showed a convex relationship with latitude,
351 indicating that phylogenetic clustering was strongest at opposite ends of the study region (Fig. 2).
352 Indeed, Mudjimba Island, the northernmost site in our study, contained species that were
353 phylogenetically clustered at deep and shallow levels of the phylogeny. In particular, Mudjimba
354 comprised many lineages from the robust clade (e.g. genera *Acanthastrea*, *Paragoniastrea*,

355 *Goniastrea*, *Dipsastrea*, *Favites*, *Pocillopora* and *Stylophora*) and contained several species within
356 most genera. Moreover, several abundant species (e.g. *Acanthastrea*) were clustered in those
357 lineages, leading to higher NRI_{ab} than NRI_{pa} values (Fig. 2). Our study was restricted to
358 subtropical and temperate latitudes and future work that examines these patterns across the entire
359 tropical-to-temperate gradient is needed to assess the importance of climatic niche conservatism in
360 shaping phylogenetic structure of coral assemblages throughout core and marginal species ranges.

361

362 Species interactions and tolerances for local environmental conditions both influence species
363 abundances. Abundance information can therefore considerably improve inferences from
364 community phylogenetic studies and improve the power to detect limiting-similarity competition
365 [47]. In our study, phylogenetic structure for several sites (i.e. Flinders Reef, Flat Rock and Cook
366 Island) changed from clustered to overdispersed when abundance information was used in the
367 analysis, highlighting the influence of biotic interactions at these sites and the importance of using
368 abundance data. For example, Flinders Reef, the most speciose of our survey sites, had the highest
369 occurrence of species from the Acroporidae family of all sites, leading to phylogenetic clustering
370 for both NRI and NTI when presence/absence data were used. However, high dominance of the
371 arborescent species *Acropora intermedia*, which occupied a large patch of the reef in a mono-
372 specific stand (site F and photo in Fig. 3), resulted in weak overdispersion at the tips of the tree
373 when species abundances were considered (NTI_{ab} < 0), pointing to the influence of biotic
374 interactions. This example highlights that abundance-weighted metrics more accurately reflect
375 assembly processes, particularly where there is high dominance of particular species with unusual
376 traits (arborescent growth was absent or rare at other sites; Fig. 3).

377

378 Phylogenetic beta diversity measures the phylogenetic distance among local assemblages and
379 allows us to connect local and regional processes [48]. Our phylogenetic betadiversity analyses
380 show that most site pairs had higher than expected phylogenetic turnover at both basal and terminal

381 levels (Fig. 4). These patterns were stronger when species abundances were considered, consistent
382 with species present at many sites but only abundant at certain sites [48]. Site pairs with high basal
383 turnover (beta_NRIpa) generally also had high terminal turnover (beta_NTIpa), but this relationship
384 was not significant for abundance-weighted data. Except for beta_NRIpa, which was greater for
385 geographically distant sites, we found no relationship between patterns in phylogenetic turnover and
386 geographic distance. Indeed, beta_NTIab was particularly high among site pairs that were
387 geographically close (within 0-3 degrees latitude or 0-300 km of each other), indicating high
388 turnover of abundant species among these sites (Fig. 4 e and f). In particular, site pairs in the
389 Solitary Islands region (30° southern latitude; Fig. S1 in supplementary material) were
390 phylogenetically most dissimilar from each other at the branch tips (Fig. 4f), even though closely
391 related species co-occurred locally (Fig. 2). These patterns of local phylogenetic clustering (Fig. 2)
392 and higher than randomly expected phylogenetic turnover (Fig. 4f) are consistent with high spatial
393 and temporal variability in environmental conditions and biological communities in this region,
394 where assemblages range from kelp- to coral-dominated [14, 16, 17].

395

396 **Conclusions and caveats**

397

398 In combination, patterns in phylogenetic alpha and beta diversity are broadly consistent with the
399 hierarchical filtering model of community assembly operating on high-latitude reefs (Fig. 1); that is
400 regional filtering of the high-latitude species pool relative to the GBR species pool (Fig. 1A-B),
401 segregation of species into local assemblages depending on the relative strength of biotic and
402 abiotic processes, and high phylogenetic turnover in this biogeographic transition zone (Fig. 1C).
403 Recent advances in coexistence theory suggest that patterns of phylogenetic clustering in
404 observational data alone can be insufficient to clearly establish the role of environmental filtering [9,
405 49, 50]. While experiments are therefore needed to tease apart the relative strength of niche and
406 competitive fitness differences among coral species, our results are consistent with findings that

407 environmental tolerance is important in structuring high-latitude coral assemblages [15, 17, 42, 43].
408 More specifically, we hypothesise that the colder, light limited and more variable environmental
409 conditions that govern coral biodiversity patterns in this region [17] impose abiotic filters at the
410 high-latitude range limits for corals. Nevertheless, our local scale analyses revealed the signature of
411 competitive processes at some sites, particularly for abundance-weighted data, highlighting the
412 importance of using abundance data when investigating assembly processes. Conservatism of tested
413 traits suggests that coral distributions will likely shift with climate change. While this is consistent
414 with recent observations of coral range expansion on high-latitude reefs in Japan [51] and Australia
415 [52], the higher than expected phylogenetic beta diversity between most site pairs recorded in this
416 study and species-specific relationships with environmental parameters [17, 53], suggest that coral
417 range shifts will likely vary among species. High phylogenetic turnover among sites highlights the
418 vulnerability and conservation significance of high-latitude reefs [14] and the need to protect a
419 substantial proportion of reefs to preserve the breadth of phylogenetic diversity in the region.

420

421 **Ethics:** Methods were approved under the University of Queensland ethics guidelines (193/10).

422 **Data accessibility:** Supporting data are freely available as electronic supplementary material.

423 **Authors' contributions:** BS, ES, MB and JMP designed the study; BS and MB collected the field
424 data; BS identified corals, performed data analysis and led the writing; all authors contributed to
425 writing the manuscript.

426 **Competing interests:** We declare we have no competing interests.

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436

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561

562 Table 1. Phylogenetic signal in ecological traits of corals in the subtropical-to-temperate transition
 563 zone in eastern Australia using Pagel's λ or D as the test statistic. P (random) and P (Brownian)
 564 indicate significance levels of departure from random and from Brownian phylogenetic structure,
 565 respectively ($P < 0.05$). Not significant departure from Brownian structure indicates conserved trait
 566 evolution.

567

| Trait | Test statistic | P (random) | P (Brownian) |
|--|-----------------------|-------------------|---------------------|
| Larval development rate | $\lambda = 0.997$ | < 0.001 | n.s. |
| Corallite size | $\lambda = 0.980$ | < 0.001 | n.s. |
| Sexual pattern (hermaphroditic / gonochoric) | $D = -0.522$ | < 0.001 | n.s. |
| Symbiont transmission | $D = -0.513$ | < 0.001 | n.s. |
| Laminar morphology | $D = -0.340$ | < 0.001 | n.s. |
| Meandroid corallite formation | $D = -0.128$ | < 0.001 | n.s. |
| Encrusting-to-massive morphology | $D = -0.160$ | < 0.001 | n.s. |
| Branching-to-tabular morphology | $D = -0.093$ | < 0.001 | n.s. |
| Reproductive mode (brood / spawn) | $D = 0.009$ | < 0.001 | n.s. |
| Ceriod corallite formation | $D = 0.033$ | < 0.001 | n.s. |
| Plocoid corallite formation | $D = 0.058$ | < 0.001 | n.s. |
| Tabular morphology | $D = 0.146$ | < 0.001 | n.s. |
| Arborescent morphology | $D = 0.554$ | 0.04 | n.s. |

568

569 **Figure captions:**

570

571 Figure 1. Conceptual representation of the hierarchical filtering assembly model tested for high-
572 latitude reefs of eastern Australia. Coral species from the Great Barrier Reef species pool (A) pass
573 through a regional filter e.g. based on species tolerances for marginal reef conditions (i.e. regional
574 high-latitude species pool) (B), and subsequently segregate into local assemblages according to
575 local biotic and/or abiotic filters that lead to clustered (more closely related) or overdispersed (more
576 distantly related than expected) phylogenetic structure (C). There is substantial turnover of lineages
577 from site to site (phylogenetic beta diversity) due to environmental gradients in the region (C).

578

579 Figure 2. Local tests for phylogenetic structure of coral assemblages arrayed along the subtropical-
580 to-temperate transition in eastern Australia, showing net relatedness index (NRI, a and c) and
581 nearest related taxon index (NTI, b and d) values using presence/absence (a and b) and abundance
582 data (c and d). Positive values indicate phylogenetic clustering and negative values reflect
583 phylogenetic overdispersion. Abbreviations for site names, with latitude increasing left to right: M
584 = Mudjimba; IG = Inner Gneerings; F = Flinders; FR = Flat Rock; CI = Cook Island; JN = Julian
585 Rocks Nursery; JF = Julian Rocks False Trench; NS = North Solitary Island; NR = North Rock;
586 NWS = North West Solitary Island; WH = Woolgoolga; SWS = South West Solitary Island; SS =
587 South Solitary Island; MB = Muttonbird Island; BR = Black Rock; CT = Cabbage Tree Island.

588

589 Figure 3. Non-parametric multidimensional scaling ordination of phylogenetic diversity patterns of
590 corals on high-latitude reefs in eastern Australia. The ordination is based on the abundance-
591 weighted net relatedness index (NRIab) and symbols represent patterns in phylogenetic structure at
592 the study sites as indicated in the legend; see Fig. 2 for abbreviations of site names. Vectors identify
593 traits that primarily discriminate assemblages: enc-mass = encrusting-to-massive morphology;
594 branch-tab = branching-to-tabular morphology; rate = larval development rate; size = corallite size.

595 Photos portray assemblage types at the study sites. All photos by B. Sommer.

596

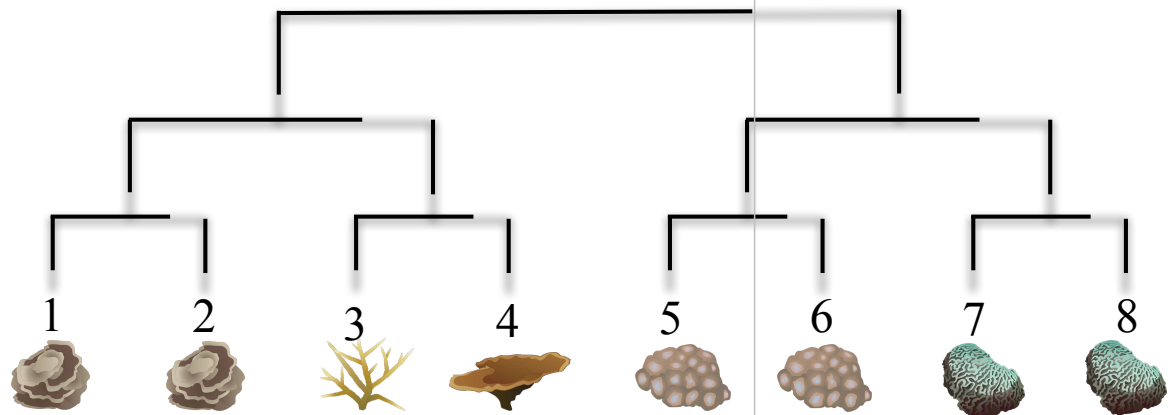
597 Figure 4. Phylogenetic betadiversity patterns of corals in the subtropical-to-temperate transition
598 zone in eastern Australia. Standardised effect sizes for beta_NRI (a-c) and beta_NTI (d-f) using
599 presence/absence (a, d) and abundance (b-c, e-f) data; pairwise turnover values plotted versus
600 geographic distance (in degrees latitude; a-b, d-e) and boxplots for site level turnover patterns (c, f).
601 The dashed line represents the expectation under a null model of random shuffling of taxa across
602 the tips of the phylogeny. Positive values indicate higher than expected turnover of species in pairs
603 of local assemblages, negative values indicate lower turnover than expected. See Fig. 2 for
604 abbreviations of site names.

A

Great Barrier Reef species pool (phylogeny)

Species (1-8)

Trait (e.g. morphology)



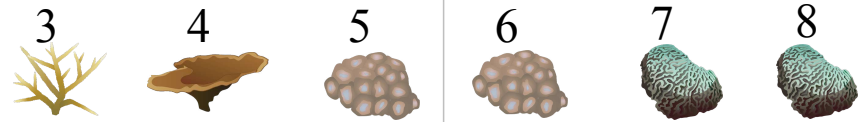
REGIONAL FILTER e.g. high-latitude climate

B

High-latitude species pool

Species

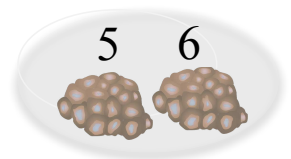
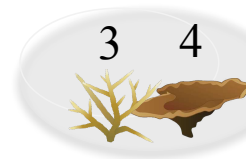
Trait



LOCAL FILTERS e.g. abiotic filtering, biotic interactions

C

Local communities (1-3)



Phylogenetic structure

overdispersed

clustered

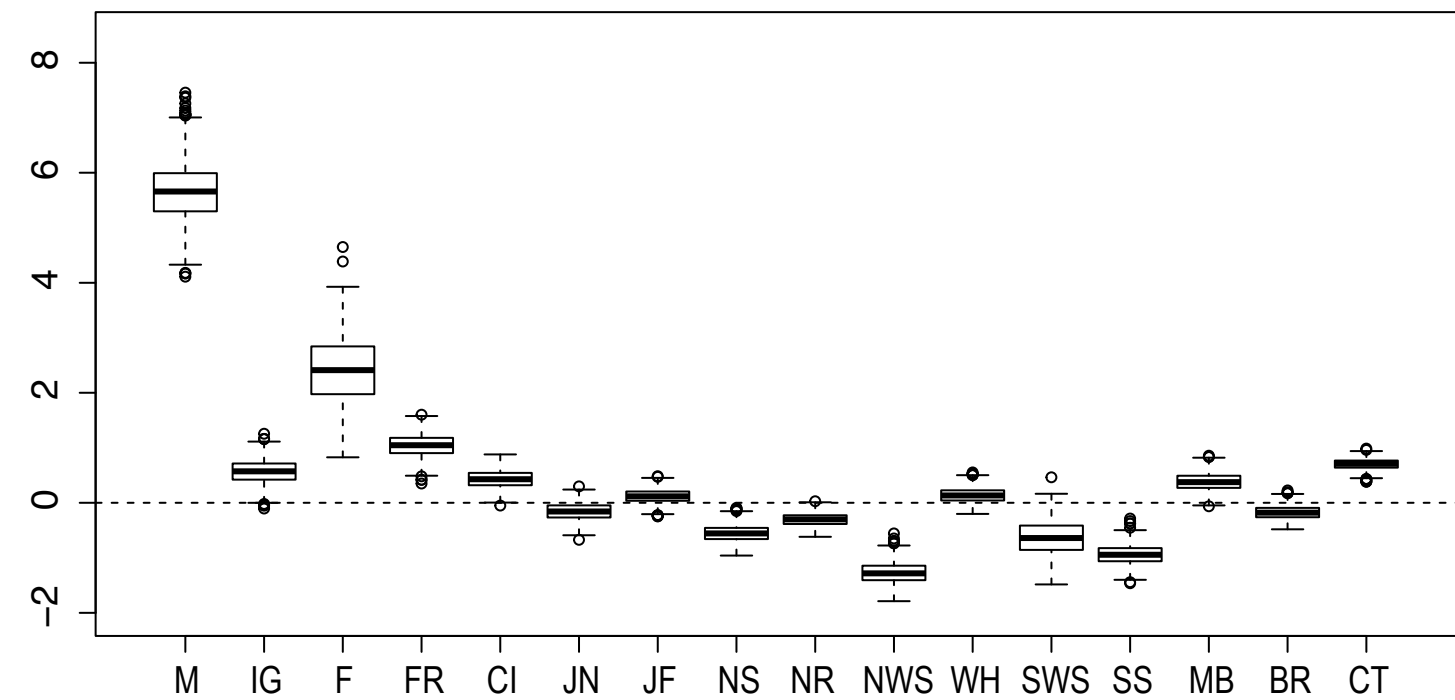
clustered

Phylogenetic beta diversity

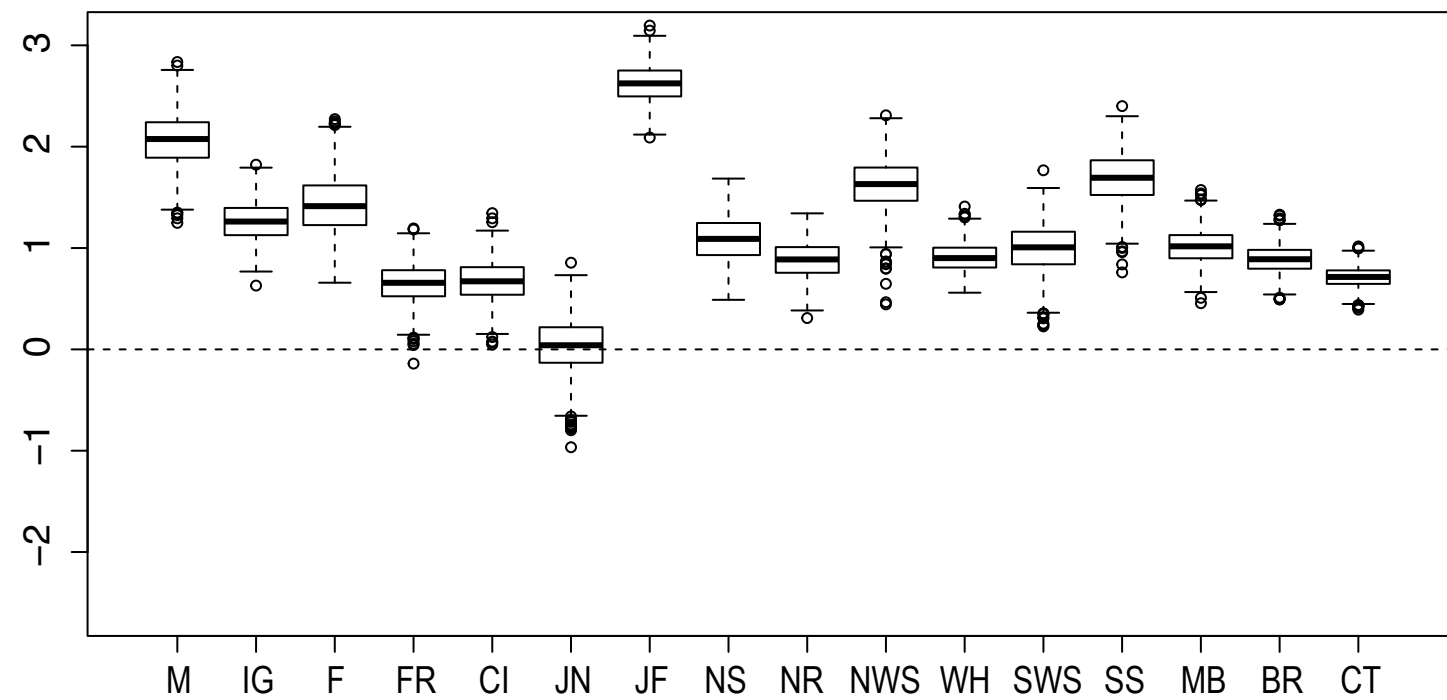
Turnover of lineages among site pairs



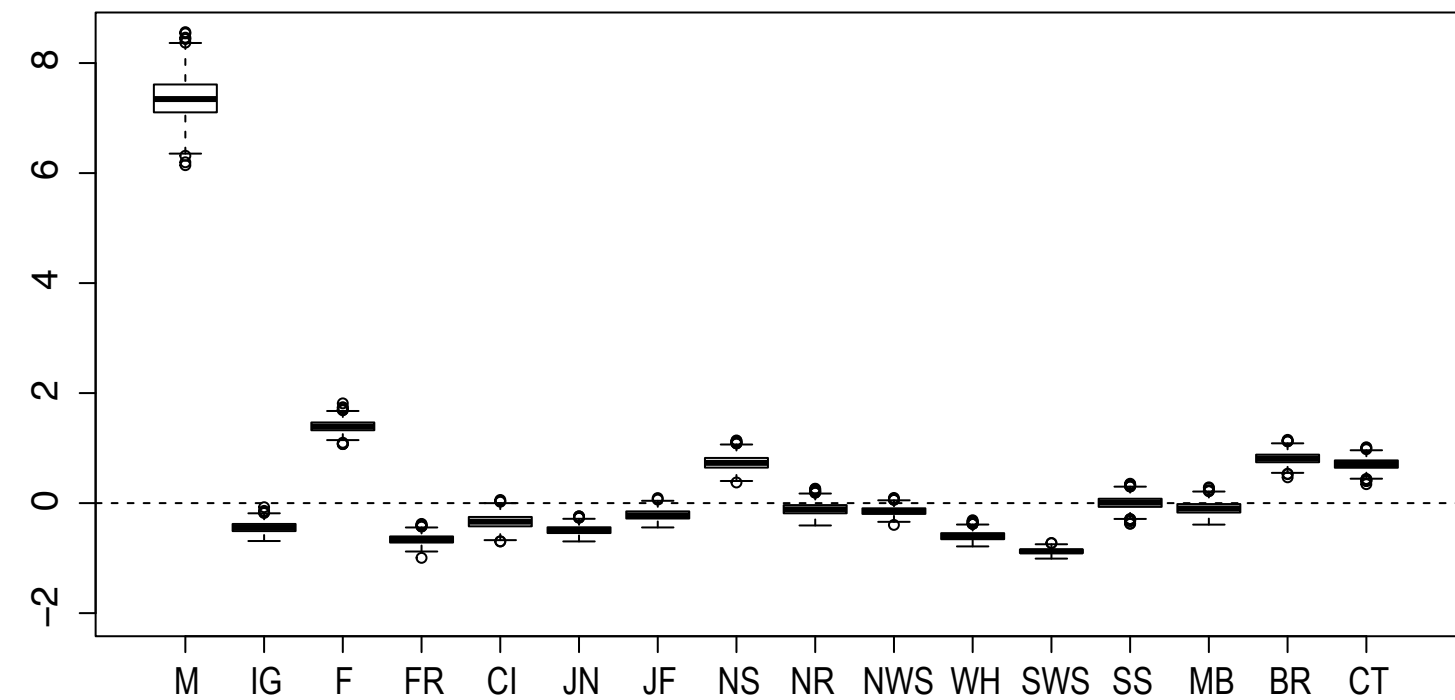
(a)



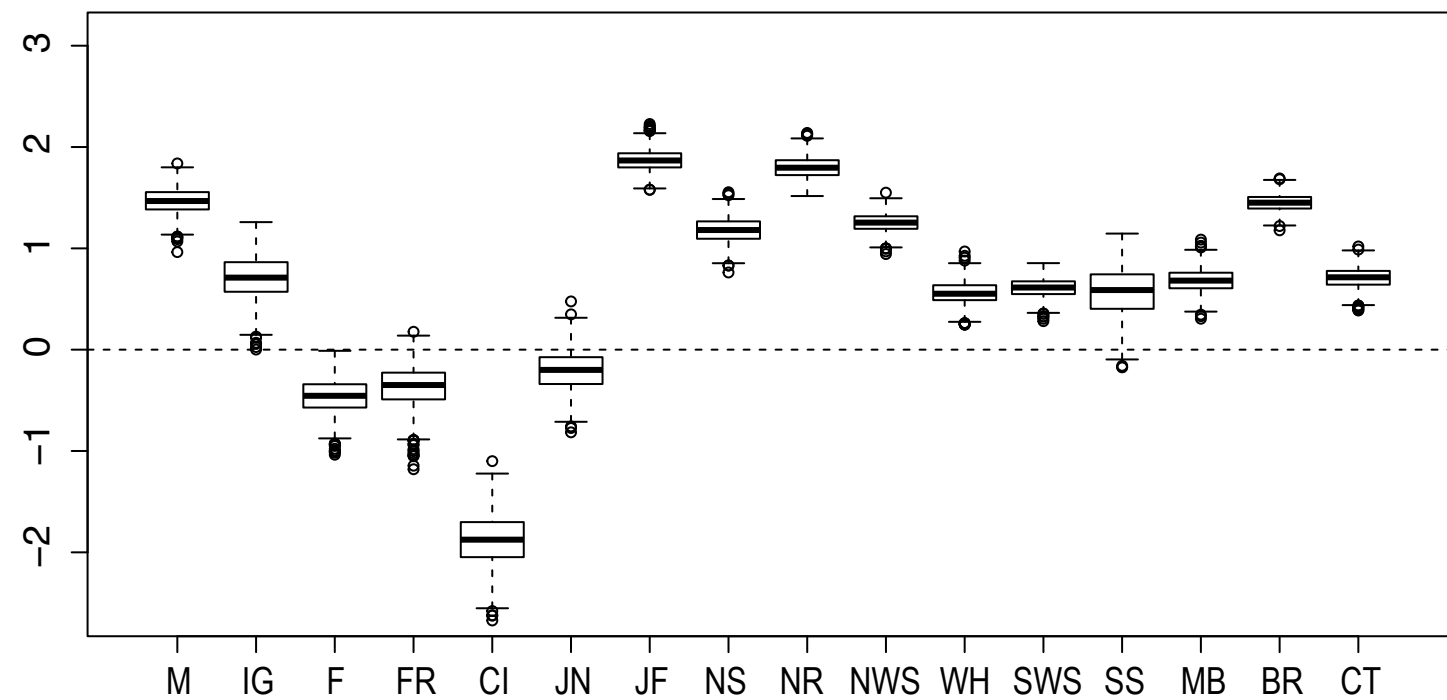
(b)



(c)



(d)



- NRI & NTI clustered
- ▲ NRI & NTI overdispersed
- ◆ NRI overdispersed, NTI clustered
- NRI clustered, NTI overdispersed

