ARTICLE

Revealing rangeomorph species characters using spatial analyses[1]

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Abstract: Rangeomorphs dominate the Ediacaran Avalonian macrofossil assemblages of Charnwood Forest, UK (~562 Ma). However, their unfamiliar fractal architecture makes distinguishing phylogenetically reliable characters from intraspecific features difficult. Fortunately, spatial analysis of large in-situ populations offers an independent means of assessing their taxonomy. Populations of a single biological species are likely to exhibit similar spatial distributions due to their shared responses to the biological and ecological processes acting upon them. As such, spatial analyses can be used to interrogate which are the most taxonomically deductive characters in similar species. We used random labelling analyses to investigate the presence or absence of characters of *Primocandelabrum boyntoni*, *P. aethelfalaedia*, and *P. aelfwynnia* on the Bed 'B'. The resultant spatial distributions were compared to observed characters using goodness-of-fit tests to determine which characters were associated with unique populations, and which were found across multiple populations. We found that *P. boyntoni* and *P. aelfwynnia* had statistically indistinguishable character distributions, suggesting that they represent a single biological species, and that they exhibited significantly different distributions to *P. aethelfalaedia*, suggesting that there are two (rather than three) species of *Primocandelabrum* present on the B surface. Furthermore, we found that the distribution of concealed versus unconcealed 1st order branches across all specimens exhibited significantly different density-dependant behaviour, with unconcealed branching occurring in areas of higher density populations and concealed branching occurring in the lower density areas of *Primocandelabrum*. We speculate that unconcealed branches may have been a response to the reduced availability of resources in higher density areas, implying rangeomorphs were capable of ecophenotypic responses.

Résumé : Les rangéomorphes dominent les assemblages de macrofossiles avaloniens de l'Édiacarien de Charnwood Forest, au Royaume-Uni (~562 Ma). Leur architecture fractale inhabituelle fait toutefois en sorte qu'il est difficile de distinguer des caractères fiables sur le plan phylogénétique d'éléments intraspécifiques. L'analyse spatiale de grandes populations in situ offre heureusement une méthode indépendante pour évaluer leur taxonomie. Les populations d'une même espèce biologique sont susceptibles de présenter des répartitions spatiales semblables en raison de leurs réactions communes aux processus biologiques et écologiques qui agissent sur elles. Des analyses spatiales peuvent donc être utilisées pour déterminer les caractères les plus déductifs sur le plan taxonomique chez des espèces semblables. Nous avons utilisé des analyses d'étiquetage aléatoire pour étudier la présence ou l'absence de caractères de *Primocandelabrum boyntoni*, *P. aethelfalaedia* et *P. aelfwynnia* sur la Bed 'B'. Les répartitions spatiales résultantes ont été comparées à des caractères observés en utilisant des tests de qualité de l'ajustement afin de déterminer quels caractères sont associés à une seule population et quels caractères sont présents dans plusieurs populations. Nous avons déterminé que *P. boyntoni* et *P. aelfwynnia* ont des répartitions de caractères statistiquement identiques, ce qui donne à penser qu'ils représentent une seule et même espèce biologique, et qu'ils présentent des répartitions significativement différentes de *P. aethelfalaedia*, ce qui indiquerait que deux (et non trois) espèces de *Primocandelabrum* se trouvent sur la surface B. Nous avons en outre déterminé que, pour tous les spécimens, les répartitions de branches primaires cachées et non cachées présentent des comportements dépendant de la densité significativement différents, les branches non cachées se trouvant dans des secteurs de populations de plus forte densité, et les branches cachées étant présentes dans des secteurs de plus faible densité de *Primocandelabrum*. Nous postulons que les branches non cachées pourraient avoir constitué une réaction à une disponibilité plus faible de ressources dans les secteurs de forte densité, ce qui indiquerait que les rangéomorphes pouvaient faire preuve de réactions écophénotypiques. [Traduit par la Rédaction]

Introduction

The Avalonian Assemblage of Ediacaran organisms contains some of the oldest known examples of macroscopic organisms in the fossil record, and is known primarily from southeastern Newfoundland, Canada (Clapham et al. 2003; Hofmann et al. 2008; Narbonne et al. 2009) and Charnwood Forest, UK (Wilby et al. 2011; Kenchington et al. 2018). Avalonian macrofossils share few simi-

larities with living taxa, making organism biology, phylogenetic relationships, and ecological interactions difficult to assess (Liu et al. 2015; Erwin et al. 2011; Xiao and Laflamme 2009). Their communities are dominated by rangeomorphs, a proposed clade of "fractally-branching" organisms (Narbonne 2004; Hoyal Cuthill and Conway Morris 2014; Erwin et al. 2011). However, their unfamiliar fractal architecture makes distinguishing phylogenetically

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Fig. 1. The plastotype (specimen 6A2l, GSM105969) of *Primocandelabrum boyntoni* from Charnwood Forest, held at the British Geological Survey, Keyworth. Scale bar = 2 cm. [Colour online.]

reliable characters from intraspecific features difficult (Liu et al. 2015; Kenchington and Wilby 2017).

One of the largest and most diverse Avalonian communities is preserved on the so-called Bed 'B' bedding-plane surface in Charnwood Forest (UK), which, at 115 m² surface area and with at least 18 different taxa, is comparable to that on the Mistaken Point E surface in Newfoundland (Canada) (Wilby et al. 2011). The multifoliate, stemmed rangeomorph *Primocandelabrum* (Hofmann et al. 2008) comprises a significant proportion of the Bed 'B' community, and is principally diagnosed by its coarse branching, the triangular outline of its crown, and by having typically rotated, unfurled folia (1st order branches) that are proximally inflated, and 2nd order branches that are typically displayed, unfurled, and medially inflated (Figs. 1 and 2; Hofmann et al. 2008; Kenchington and Wilby 2017). Prior statistical analyses by Kenchington and Wilby (2017) used multivariate cluster analyses to formally describe three species of *Primocandelabrum* using both continuous (e.g., length to width ratios) and discreet (e.g., rotated 1st order branches, Fig. 2) characters, and revealed a hitherto unrecognized morphological variability in *Primocandelabrum*. Within the Kenchington and Wilby results there is overlapping variation between the individuals in the clusters (Fig. 3), with individuals in different clusters sharing some of the same characters and some characters not being 100% unique to a cluster. Their analyses suggested two or three species of *Primocandelabrum*: *P. boyntoni*, *P. aelfwynnia*, and *P. aethelflaedia*. As such, there remains uncertainty regarding the number of species present on Bed 'B'.

The preservation of Avalonian macrofossil communities may be exceptional, with notable examples of thousands of these organisms preserved in-situ on successive bedding planes (Wood et al. 2003; Kenchington and Wilby 2014; Liu et al. 2015). Their sessile habit and their preservation in life position means that their position on a bedding plane encapsulates their life-history: that is, their position is a combined record of the abiological, biological, and ecological processes that impacted them during their life. Consequently, spatial analyses can be used to investigate otherwise cryptic aspects of Ediacaran life, such as how they reproduced (Mitchell et al. 2015) or how they interacted with each other (Mitchell and Kenchington 2018) and (or) their environment (Mitchell and Butterfield 2018), and to provide a complimentary record to prior ecological analyses of population size–frequency distributions (Darroch et al. 2013; Wilby et al. 2015).

There are four types of processes that control population spatial distributions for extant sessile organisms: (1) dispersal processes, (2) associations with local habitat heterogeneities, (3) direct interspecific interactions, and (4) de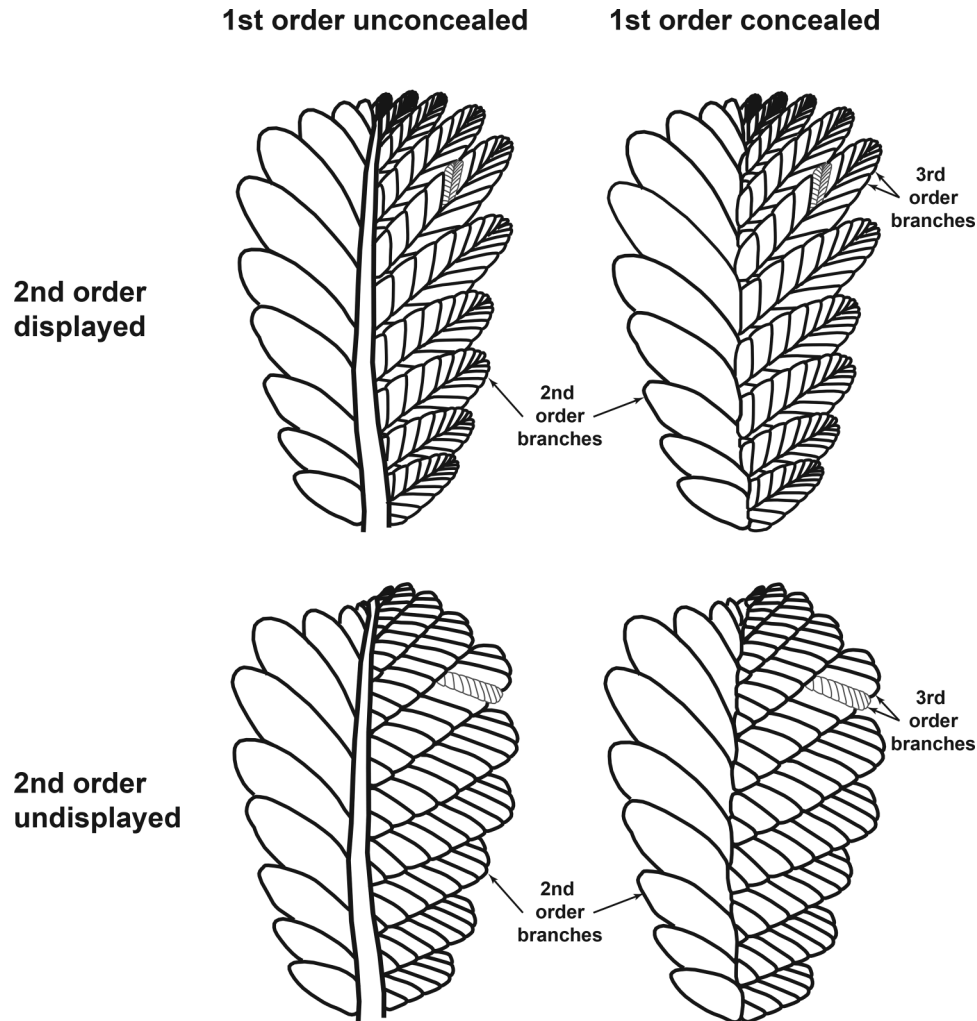nsity-dependent effects (Wiegand et al. 2007b). The first three represent inter-specific interactions and these can have either a negative impact on populations, such as competition for limited resources, or a positive impact, such as facilitation, whereby one species enhances the survival of another. Density-dependent effects include, for example, Janzen–Connell effects, whereby a specialist consumer, such as a pathogen or a taxon-specific herbivore, leads to density-dependent deaths (Velázquez et al. 2016). In non-motile systems, such as the Avalonian ones, density-dependent effects are limited to pathogens because macroscopic predators and herbivores are absent (e.g., Liu et al. 2015). Pathogens transfer between organisms in high-density areas more easily than between those in low-density areas, thus creating differential mortality patterns based on relative density (Wiegand et al. 2007a). Significant density-dependent mortality can be detected via the spatial distributions of taphomorphs, such as ivesheadiomorphs, and (or) by the incorporation of effaced characteristics into analyses (cf. Mitchell and Butterfield 2018). Consequently, well preserved specimens, such as those considered in the present study, can be assumed to not have been significantly impacted by pathogenic mortality effects and, hence, only the first three processes need be considered.

Each of the three inter-specific processes have numerous factors that impact the resultant spatial distributions. The spatial distributions induced by dispersal processes are determined by the following factors: the type of dispersal process (e.g., propagule or stolonifereous), the number of offspring, the height at which propagules are released, the current speed (which is assumed conserved across a given community at a given time), and the relative density of the settled offspring (e.g., Yamamichi et al. 2014). Habitat influences can vary within any one habitat by operating at different spatial scales, having a positive or negative impact, and (or) varying in their relative strength (Wiegand et al. 2007b), as can interspecific interactions (Lingua et al. 2008). Acting in combination, these factors produce an enormous number of possible different combinations of spatial distributions: just taking each factor as discrete (which would be a very simplified model, since only 2/11 of the characters are discreet) would give almost 40 million different possible combinations. Consequently, if two populations exhibit the same spatial distribution, it is reasonable to infer that the same abiological, biological, and ecological processes have impacted both populations. This situation is most likely to happen when the two populations are, in fact, just a single species.

Spatial analyses have previously been used within the Avalon Assemblage to investigate the possible taxonomic affiliations of enigmatic forms referred to as ivesheadiomorphs and lobate discs (Mitchell and Butterfield 2018). These have variously been suggested to be either the decayed remains of other taxa (i.e., taphomorphs, Liu et al. 2011), microbial colonies that were independent of macro-organisms or their carcasses (cf. Laflamme et al. 2012), sediment load structures (Wilby et al. 2011), or a combination of these (Kenchington et al. 2018). Comparison of the spatial distributions of the populations of ivesheadiomorphs and lobate discs on the E surface of Mistaken Point revealed that the ivesheadiomorphs were most likely the taphomorphs of *Fractofusus* and *Charniodiscus*, while lobate discs were found to most likely not be the taphomorphs of any of the other taxa on the surface (Mitchell and Butterfield 2018).

In this study, we extend the use of spatial analyses to interrogate what constitute the most taxonomically informative characters in a single rangeomorph genus. We test the impact of morphological characters on taxonomic differences by assuming that if two named species differ by a single morphological character but exhibit the same spatial distributions then that character is unlikely to be taxonomically significant and more likely represents a differential response to some stimulus. We use spatial analyses to test current taxonomic definitions for multifoliate taxa on Bed 'B', contrasting each of the three proposed species of *Primocandelabrum* with another abundant multi-foliate rangeo-

Fig. 2. Categorical characters of 1st order branching. When the 1st order branch is unconcealed, the stalk is visible (left hand side), while it is hidden if concealed (right hand side). When the 2nd order branch is displayed (unfurled) both rows are visible (top row), while branch edges are tucked to give a smooth outer margin when the 2nd order branch is rotated (or furled).

1st order unconcealed   **1st order concealed**

2nd order displayed

3rd order branches

2nd order branches

2nd order undisplayed

3rd order branches

2nd order branches

morph (the "dumbbell" of Wilby et al. 2015). We also investigate whether specific characters, such as branching concealment and rotation (Fig. 2), exhibit density-dependant behaviour.

Data

Characters were assigned to *Primocandelabrum* and dumbbell specimens using the data from Kenchington and Wilby (2017). Fourteen discrete (i.e., categorical) *Primocandelabrum* characters are recognised, of which six are not consistently preserved and another six were the same across almost all specimens (i.e., only <2 specimens exhibited a different character). Thus, there are only two discrete characters that show variability within each of the three species of *Primocandelabrum*: 1st order branch concealment or unconcealment and 2nd order radiating or subparallel branch arrangement (Fig. 2; Table 1).

A spatial map was constructed of the Bed 'B' community using Reflectance Transformation Images (RTI) of ~1 m × 1 m casts of the surface (Kenchington et al. 2018). These were placed in their correct spatial positions by georeferencing them to a LiDAR scan of the entire surface. Each specimen was then assigned its morphological characters and taxonomic identity (Table 1), and these characters were then compared using random labelling spatial analyses (cf. Mitchell and Butterfield 2018).

Methods

Previous work on Ediacaran spatial ecology has focussed on investigating the processes that led to the fossil positions, such as dispersal, habitat associations, or resource competition (Mitchell et al. 2015; Mitchell and Butterfield 2018; Mitchell and Kenchington 2018). In this study, we are not investigating the origination of fossil positions, but we are instead concerned with the spatial distributions of characters within those fossil locations. This requires a different approach, and relies on random labelling analyses (RLAs) (Jacquemyn et al. 2010; Raventós et al. 2010). RLAs are a type of spatial point process analysis whereby random models are simulated whilst the positions of the specimens remain the same and a given character state, such as species definition or nature of rangeomorph branching (Fig. 4), is repeatedly permutated (Fig. 4). Figures 4A–4C illustrate the concept: the points remain in the same place, but the colour allocated to them (representing different character states) is changed. Applied to Bed 'B', the fossil locations stay the same, but whether each fossil exhibits concealed 1st order branching or not, for example, is changed randomly in each simulation. As such, RLAs do not directly measure the aggregation or segregation between two populations, so they do not test the processes that resulted in

Fig. 3. Results of the Kenchington and Wilby 2017 cluster analysis using categorical and continuous characters for the species of *Primocandelabrum*. (A) Cluster dendrogram and (B) factor map for analysis on continuous and categorical characters. Inertia gain plots support division into two or three clusters in (A). Schematic diagrams describe the clusters that match their colour. [Colour online.]
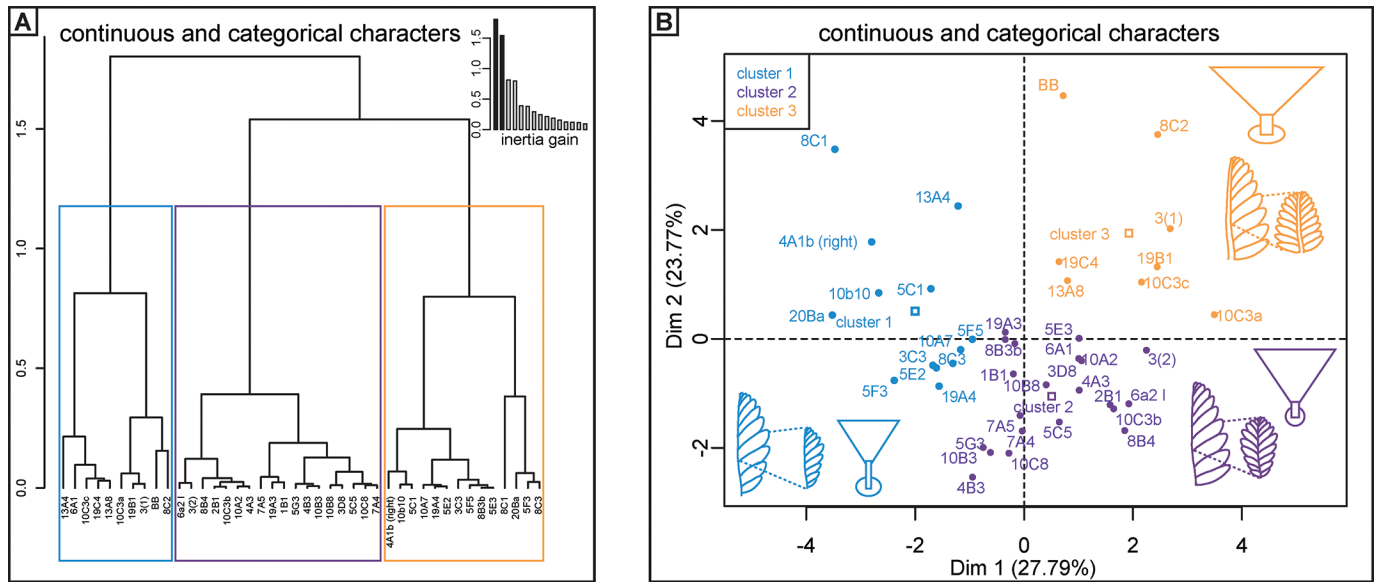
fossil location, but instead measure the differences in spatial distributions of characters between two populations.

Spatial distributions are commonly described using pair correlation functions (PCFs) that describe how the density of points (i.e., fossil specimens) changes as a function of distance (e.g., Illian et al. 2008). RLAs assess the differences between two characters of the populations by calculating variations between PCFs by considering the Difference and Quotient tests (Wiegand and Moloney 2013). The Difference test is the calculation of the distribution of $PCF_{11} - PCF_{22}$, where PCF_{11} is the univariate PCF for group 1 and PCF_{22} is the univariate PCF for group 2. If $PCF_{11} - PCF_{22} = 0$, then both groups are randomly distributed within the locations (i.e., both groups exhibit the same spatial behaviour). If $PCF_{11} - PCF_{22} > 0$, then group 1 is more aggregated than group 2; if $PCF_{11} - PCF_{22} < 0$, then group 2 is more aggregated than group 1. The Quotient test calculates the bivariate PCF between groups relative to the pattern of both groups taken together (the joined pattern), where PCF_{12} is the bivariate distribution of group 2 relative to group 1 and PCF_{21} is the bivariate distribution of group 1 relative to group 2. For joint patterns, $PCF_{1,1+2}$ is the bivariate distribution of group 1 relative to both groups together, and $PCF_{2,2+1}$ is the bivariate distribution of group 2 relative to the joint pattern. Thus, the Quotient test is the calculation of the distribution: $PCF_{1,1+2} - PCF_{21}/PCF_{2,2+1}$, where $PCF_{12}/PCF_{1,1+2} - PCF_{21}/PCF_{2,2+1} > 0$ indicates that group 2 is mainly located in areas with high density of the joint pattern, and group 1 is in low density areas (i.e., that group 2 has more neighbours than group 1). If this quotient is significantly nonzero, then the process underlying the characters is density-dependent; for example, concealment occurs more commonly in high-density areas.

Establishing whether the null hypotheses of the Difference and Quotient tests should be rejected or not is complicated, because there is a lack of independence of the spatial points (fossil positions) and variety of different point pattern distributions (Illian et al. 2008). Two different methods are commonly used to establish acceptance or rejection of the null hypotheses for ecological data (e.g., Wiegand and Moloney 2013 and references therein): (1) Monte Carlo simulations (Illian et al. 2008), and (2) Diggle's goodness-of-fit test p_d, which represents the total squared deviation between the observed pattern and the stimulated pattern across the studied distances (Diggle 2003). The two comparisons

are used together because (*i*) the Monte Carlo simulation envelopes do not necessarily correspond to confidence intervals, and they run the risk of Type I errors if the observed PCF falls near the edge of the simulation envelope (Illian et al. 2008); (*ii*) The p_d does not strictly test whether a model should be accepted or rejected, but rather whether the test calculation for the observed data are within the range of the stochastic realization of the null hypothesis (Diggle 2003); and (*iii*) The p_d depends on the range over which it is calculated, meaning that the model may not fit at very small distances due to the physical occupation of that space by the organisms themselves, but may fit well at larger distances (Diggle 2003; Illian et al. 2008). Thus, visual inspection of the PCFs with Monte Carlo simulation envelopes, coupled with p_d, ensures that these errors are minimized. The underlying mathematics is described in detail by Wiegand and Moloney (2004) and Wiegand et al. (2006).

Here, we test six null hypotheses (H_0) using RLA of character or species data and the specimen positions on the Bed 'B' surface:

(1) H_0^{Sp}: Species of *Primocandelabrum* do not exhibit significantly different spatial distributions (PCFs) to that of the dumbbell taxon.

(2–4) H_0^{boyn}; H_0^{aeth}; H_0^{aelf}: The bivariate PCFs of the three species of *Primocandelabrum*, *P. boyntoni*, *P. aethelfalaedia*, and *P. aelfwynnia*, do not differ significantly from each other.

(5) $H_0^{concealed}$: The spatial distributions of concealed or unconcealed 1st order branches are not significantly different.

(6) $H_0^{radiation}$: The spatial distribution of radiation versus sub-parallel 2nd order branches are not significantly different.

The following RLAs were conducted using Programita software (Wiegand and Moloney 2004; Wiegand et al. 2006, 2009, 2012):

(1) To test H_0^{Sp}, the univariate PCFs of the species of *Primocandelabrum* and of the dumbbell taxon (PCF_{11} and PCF_{22}) were calculated by creating a distribution map of each taxon according to a 1 cm × 1 cm grid of the Bed 'B' surface within which the taxon density was calculated. The Difference test was then performed between the two groups.

(2) To test H_0^{boyn}, H_0^{aeth}, and H_0^{aelf}, the Difference test was performed between the named species group and the other two species grouped together. Two species were grouped together to enable a sufficient sample size to run the analyses. If a pair of

Table 1. Summary of data used in this study, taken from Kenchington and Wilby (2017).

Specimen ID	Species ID	1st concealed?	2nd radiating?
10C3c	*Primocandelabrum aelfwynnia*	Unconcealed	Subparallel
3(1)	*P. aelfwynnia*	Unconcealed	—
3(2)	*P. aelfwynnia*	Unconcealed	Radiating
3D8	*P. aelfwynnia*	Concealed	Subparallel
8B3b	*P. aelfwynnia*	Concealed	Radiating
8C2	*P. aelfwynnia*	Unconcealed	Radiating
Big Bertha	*P. aelfwynnia*	—	Subparallel
5E2	*P. aethelflaedia*	Concealed	Subparallel
10B10	*P. aethelflaedia*	Concealed	Radiating
10C4	*P. aethelflaedia*	—	—
3C3	*P. aethelflaedia*	Concealed	Radiating
4A1b (right)	*P. aethelflaedia*	Concealed	Subparallel
5C1	*P. aethelflaedia*	—	—
5F3	*P. aethelflaedia*	Concealed	Subparallel
5F5	*P. aethelflaedia*	Concealed	—
5E3	*P. boyntoni*	Concealed	Radiating
10B3	*P. boyntoni*	Concealed	Radiating
10B8	*P. boyntoni*	Concealed	—
10C3b	*P. boyntoni*	Unconcealed	Subparallel
10C8	*P. boyntoni*	Concealed	Subparallel
13A8	*P. boyntoni*	—	Radiating
1B1	*P. boyntoni*	Unconcealed	Radiating
2B1	*P. boyntoni*	Unconcealed	—
4A3	*P. boyntoni*	Unconcealed	Subparallel
4B3	*P. boyntoni*	Concealed	Radiating
5C5	*P. boyntoni*	—	—
5G3	*P. boyntoni*	—	—
6a2l	*P. boyntoni*	Unconcealed	Radiating
7A4	*P. boyntoni*	Concealed	—
7A5	*P. boyntoni*	Unconcealed	Subparallel
8B4	*P. boyntoni*	Unconcealed	Subparallel
5A4	Dumbbell	Concealed	—
3D7	Dumbbell	Concealed	—
5C6	Dumbbell	Concealed	Radiating
3E1(1)	Dumbbell	Concealed	Radiating
8C1	Dumbbell	Unconcealed	Subparallel
10C3c	*P. aelfwynnia*	Unconcealed	Subparallel
3(1)	*P. aelfwynnia*	Unconcealed	—
3(2)	*P. aelfwynnia*	Unconcealed	Radiating
3D8	*P. aelfwynnia*	Concealed	Subparallel
8B3b	*P. aelfwynnia*	Concealed	Radiating
8C2	*P. aelfwynnia*	Unconcealed	Radiating
Big Bertha	*P. aelfwynnia*	—	Subparallel
5E2	*P. aethelflaedia*	Concealed	Subparallel
10B10	*P. aethelflaedia*	Concealed	Radiating
10C4	*P. aethelflaedia*	—	—
3C3	*P. aethelflaedia*	Concealed	Radiating
4A1b (right)	*P. aethelflaedia*	Concealed	Subparallel
5C1	*P. aethelflaedia*	—	—
5F3	*P. aethelflaedia*	Concealed	Subparallel

Note: Spatial data is available on request from the lead author.

species has significantly the same spatial distributions, as would be expected if they were one species and not two, then we should expect that there is not a significant difference between spatial distributions that incorporate either of the species. For example, if species A and B are the same and C is a different species, the spatial distributions of A + B will differ to C. Furthermore, if either A or B is incorporated into a grouping with C and then compared against the remaining species (e.g., A + C compared to B), the result will not be significantly different because the pattern of A will mask any differences to C.

(3) To test $H_0^{\text{concealed}}$, the Difference test was used to assess whether there was a significant difference between the PCFs of each species, and the Quotient test was used to assess whether any of the differences found were depended on specimen density.

(4) To test $H_0^{\text{radiation}}$, the Difference and Quotient tests were used to assess whether the spatial distribution of 2nd order radiating or displayed varied regardless of taxonomic affinity.

Each hypothesis was tested by running 999 Monte Carlo simulations for each group to generate simulation envelopes around the random model (i.e., $\text{PCF}_{11} - \text{PCF}_{22} = 0$). p_d values were calculated using Diggle's goodness-of-fit test (Diggle 2003). A total of 999 simulations were run (instead of 1000, for example) because the p_d value is calculated using the model simulation data (not the theoretical model), so by using 999 the p_d simulations could be measured in 0.001 increments. If the observed $\text{PCF}_{11} - \text{PCF}_{22}$ fell outside the RLA simulation envelopes and had $p_d < 0.1$, then the distributions were found to be significantly different.

Random labelling analyses hold the positions of the specimens constant so that if taphonomic processes (cf. Kenchington and Wilby 2014) impact all groups similarly, as might reasonably be expected for mutually aligned and simultaneously buried specimens (see Wilby et al. 2011, 2015), then they are independent of the RLAs. This property of RLAs means that a subsample of the total population can be analysed. Our data are a subsample of the total population of multifoliate rangeomorphs on Bed 'B' (only well-preserved specimens were used), so only differences between spatial distributions of specimen positions and density dependence can be tested. Examination of species dispersal and (or) inter-specific interactions (cf. Mitchell et al. 2015; Mitchell and Butterfield 2018) require the whole population, so they are not considered here.

Results

We reject null hypothesis H_0^{Sp} because the low p_d value and excursions outside of the simulation envelope from the Difference test shows that *Primocandelabrum* versus non-*Primocandelabrum* had significantly different spatial patterns ($p_d = 0.057$; Fig. 5A). H_0^{aeth} is also rejected because *P. aethelfalaedia* had a significantly different spatial pattern to *P. boyntoni* and *P. aelfwynnia* ($p_d = 0.083$; Fig. 5B). H_0^{boyn} and H_0^{aelf} are accepted because no significant difference was found for either *P. boyntoni* or *P. aelfwynnia* ($p_d \gg 0.1$). $H_0^{\text{radiation}}$ is also accepted: there is no difference in spatial distributions between the presence of 2nd order radiating or subparallel branching ($p_d \gg 0.1$). $H_0^{\text{concealed}}$ is rejected because concealed versus unconcealed 1st order branches exhibit significantly different spatial distributions ($p_d = 0.024$; Fig. 5C) and density dependant behaviour ($p_d = 0.035$; Fig. 5C). Unconcealed branching occurrs in the higher density areas, and concealed 1st order branching occurs in the lower density areas. The p_d value for $H_0^{\text{concealed}}$ is smaller than those found between different species, suggesting that the spatial signal of concealment is stronger than that of the constituent species and, consequently, that the differences are not taxonomically controlled.

Discussion

Currently, there is no consensus regarding the taxonomic value of particular rangeomorph characters and there are competing taxonomic schemes in operation (Brasier et al. 2012; Laflamme et al. 2012; Liu et al. 2016). This study presents a methodology for assessing the utility of discreet characters in rangeomorph taxonomy that is independent of specimen morphology, with important implications for rangeomorph taxonomic identification, Ediacaran species richness analyses, and identification of phylogenetically useful rangeomorph characters.

Species of *Primocandelabrum* on Bed 'B'

For sessile organisms, there are four different types of processes that impact their spatial distribution: physical environ-

Fig. 4. Random labelling analyses concept. Two character states are denoted by the grey and black circles. The positions of the circles remain constant, but the character state associated with each circle is randomly changed using Monte Carlo simulations (A–D). The pair correlation functions (PCFs) for each simulation are calculated and used to generate the upper and lower boundaries expected if the character states were randomly distributed over the positions.
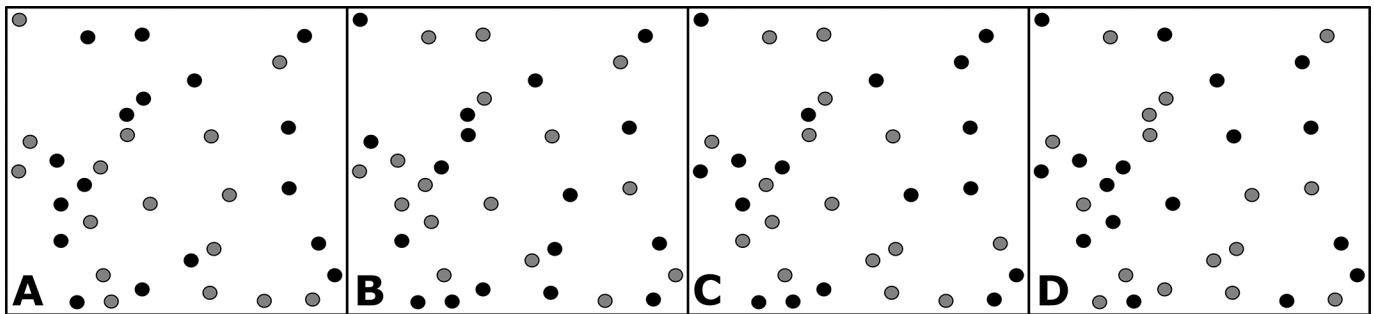
ment (Wiegand et al. 2007*a*), organism dispersal or reproduction (Seidler and Plotkin 2006), interspecific interactions, such as competition for resources (Getzin et al. 2006) and (or) facilitation (Lingua et al. 2008), and differential mortality processes, such as Janzell–Cornell effects (Getzin et al. 2008). The combination of these different processes rarely impacts two species populations in exactly the same way: for example, while two species may respond similarly to a local environmental heterogeneity, their dispersal processes are most likely different. As such, while it is never possible to be 100% certain about the underlying processes behind spatial distributions (Lin et al. 2011; Wiegand and Moloney 2004; Wiegand et al. 2007), one can be confident that if two species have the same spatial distributions they are most likely to be formed by the same underlying processes, and thus they are most likely to be a single species. This approach is verified for Ediacaran populations by the fact that the dumbbell taxon and the species of *Primocandelabrum* exhibit significantly different spatial distributions (Fig. 5A).

Prior analyses suggested that there are either two or three species of *Primocandelabrum* on Bed 'B' (Fig. 3; Kenchington and Wilby 2017) and that the morphological distinctiveness of *P. aethelflaedia* is greater than the morphological differences between *P. boyntoni* and *P. aelfwynnia* (Fig. 5B). Our analyses confirm this result by an independent means, finding that *P. aethelflaedia* exhibits significantly different spatial distribution compared to *P. boyntoni* and *P. aelfwynnia*. The similarities in the spatial behaviour of *P. boyntoni* and *P. aelfwynnia* suggests that they were most likely subject to the same processes, which is most consistent with them being one taxon, not two. As such, their synonymization should be considered.

Species richness estimates

Ediacaran organisms provide the earliest evidence of complex life and underpin our understanding of early radiations and possible extinction within the animal kingdom over the Ediacaran to Cambrian transition (e.g., Shen et al. 2008; Darroch et al. 2013). Key to this is a reliable means of determining species richness. With only relatively few Ediacaran taxa described globally (~124 taxa; Boag et al. 2016), Ediacaran macro-evolutionary patterns are particularly sensitive to small changes in species richness. The accuracy of such diversity studies depends on accurate taxonomic frameworks, which are currently in a state of flux (e.g., Laflamme at al. 2012; Liu et al. 2016). This study demonstrated that there are most likely two, not three, species of *Primocandelabrum* present on Bed 'B'. If this situation is at all representative, it is possible that Avalonian taxonomic diversity has been inflated (~25 species are currently described; Liu et al. 2015) and, thus, that the species richness of these early complex communities has been overestimated.

Ecophenotypism

The identification of phylogenetic, ontological, and (or) ecophenotypic characters is especially difficult for rangeomorphs because they are endemic to the Ediacaran time period, with only a couple of putative Ediacaran survivors (e.g., Muscente et al. 2018). We find that the concealment of 1st order branches is strongly density dependent, with concealment occurring in the low density areas of the community and unconcealment in the high density areas. Concealment of a branch is defined when the central axis covered by its secondary branches so is not visible (Brasier et al. 2012), and may be related to the efficiency of branch packing. In high density areas, competition for resources (such as water-column nutrients or neighbour shading) is likely to be more intense (e.g., Tanner et al. 2009), and organisms may adapt in ways that are not beneficial in lower densities areas. Theoretically, packing efficiency could be compromised to increase the exposure of branches to the water column, and therefore enhance nutrient uptake. We postulate that concealed 1st order branches may have allowed sufficient nutrient uptake in low-competition areas but, in areas of higher competition, having unconcealed 1st order rangeomorph branches outweighed the advantages of more efficient branch packing. Alternatively, it is possible that 1st order concealment does not record an in-life response to differing community densities, but rather a taphonomic artefact induced by different fluid flow conditions within communities of different density (cf. Ghisalberti et al. 2014). Currently, the underlying process(es) behind the response remain uncertain.

There is no direct correlation between concealment and taxonomic assignment within *Primocanelabrum*: all three species of *Primocandelabrum* exhibit both concealed and unconcealed 1st order branches. However, different taxa may have had different abilities to conceal their branches, so while our analyses show that concealment could be an environmental response, it may also have a weak taxonomic signal. Whatever the cause, because the density signal of concealment imparts a much stronger signal than any taxonomic one, this character should be used with caution when defining taxa and investigating rangeomorph phylogenies (cf. Dececchi et al. 2017). In contrast, the radiation of the 2nd order branches does appear to be a biological signal.

Utility of spatial analyses for taxonomic investigations

This study provided a way to assess taxonomic identity that is independent of multivariate morphological analyses commonly employed for rangeomorphs (e.g., Gehling and Narbonne 2007; Laflamme et al. 2004; Laflamme and Narbonne 2008). Our results strongly support previous morphological analyses of the same populations of *Primocandelabrum* on Bed 'B' (Kenchington and Wilby 2017). These analyses enable investigation of environmental impact on characters beyond previous morphological analyses. While

Fig. 5. Random labelling analysis (RLA) plots of all significantly non-random analyses. The distance in metres is given by the *x*-axis and the result of either the pair correlation function (PCF) difference or quotient is given by the *y*-axis. The *y* = 0 corresponds to a random distribution between groups (either species or characters). Observed data are given by the black line. The grey area represents 999 RLA Monte Carlo simulations. (A) H_0^{Sp} RLA Difference test showing a significantly different spatial distribution between species of *Primocandelabrum* and the dumbbell taxon. (B) H_0^{aeth} Difference test showing *P. aethelfalaedia* has a significantly different spatial pattern to that of *P. boyntoni* and *P. aelfwynnia*. (C) $H_0^{concealed}$ Quotient test showing density dependent behaviour of the 1st order concealment.
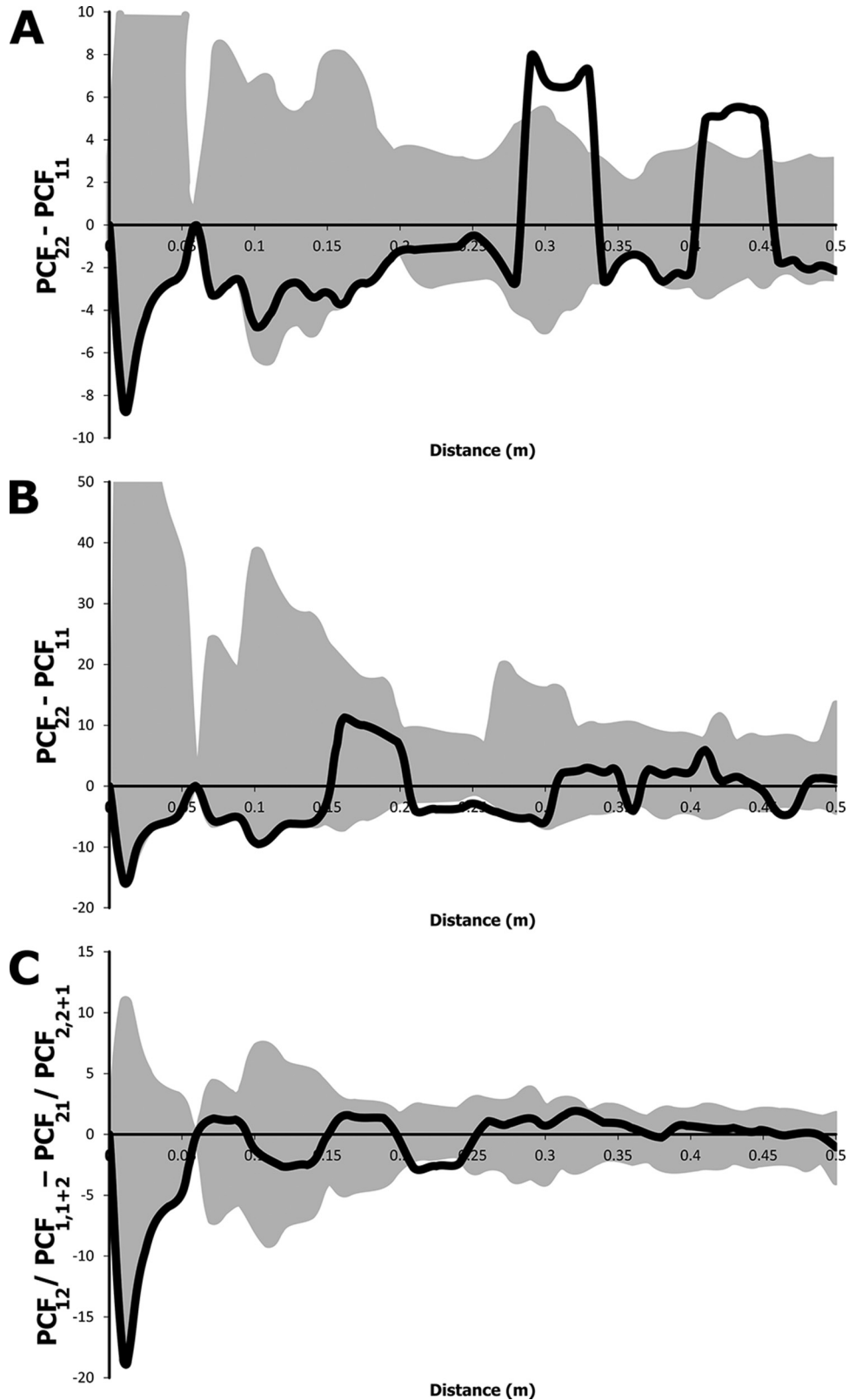
previous analyses demonstrated that concealment of 1st order branches was a useful discreet character by which to help discriminate species of *Primocandelabrum* from each other and from dumbbell taxon (as dumbbell is very rarely unconcealed), we instead found that the variation of concealment within all taxa (both dumbbell and *Primocandelabrum*) was strongly dependent on specimen density, much more so than with taxonomic affinity. Thus, the RLAs have found a hitherto unknown signal that was not possible to identify from morphological analyses alone. It highlights the potential for other characters, both discreet and continuous, to be taxonomically irrelevant.

Conclusions

Detailed analyses of species of *Primocandelabrum* suggests that there are most likely two, not three, different species of *Primocandelabrum* present on the Bed 'B' surface of Charnwood Forest. This result is consistent with previous work using morphological statistical analyses, which found *P. aethelfalaedia* to be the most different of the species of *Primocandelabrum* (Fig. 2; Kenchington and Wilby 2017), thus presenting an independent method of confirming morphological analyses. We have shown that there is significant density dependence as to whether 1st order branches are concealed or unconcealed. Specimens with unconcealed primary branches were found to occupy the higher-density areas of the *Primocandelabrum* community, while specimens with concealed primary branches occupied the lower density areas. This signal is distinct from the taxonomic results, which identified the concealed or unconcealed character as being taxonomically useful. Our findings suggest that all of the studied multi-foliate rangeomorphs had the potential to exhibit unconcealed 1st order branches in high density areas, demonstrating the capacity of rangeomorphs to respond to their local environment.

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