The relative influence of niche versus neutral processes on Ediacaran communities

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Abstract

A fundamental question in community ecology is the relative influence of niche versus neutral processes in determining ecosystem dynamics. The extent to which these processes structured early animal communities is yet to be explored. Here we use spatial point process analyses (SPPA) to determine the influence of niche versus neutral processes on early total-group metazoan paleocommunities from the Ediacaran Period ~565 million years in age. Preservation of these sessile organisms in large in-situ populations on exposed bedding planes enables inference of the most likely underlying processes governing their spatial distributions by SPPA. We conducted comprehensive spatial mapping of six of the largest Ediacaran paleocommunities in Newfoundland, Canada and Charnwood Forest, UK using LiDAR, photogrammetry and a laser-line probe. For each paleocommunity we determined the best-fit spatial model for each univariate and bivariate species distribution, comparing four sets of spatial models (complete spatial randomness, dispersal, habitat, and combined dispersal with habitat) using goodness-of-fit tests. Random and dispersal models are considered neutral processes while habitat and combined models are considered niche processes. We find the dynamics of these paleocommunities to be dominated by neutral processes, with limited influence from niche processes. Our findings are consistent with community model predictions of when neutral dynamics dominate, but are in stark contrast to the niche-dominated communities of the modern marine realm. Thus, while the underlying processes determining metazoan community assembly appear to have been in place since the appearance of the first macroscopic, complex animals, the dynamics of these early metazoan communities were fundamentally different to those of extant communities.

Significance statement

The extent to which habitat and dispersal processes structure the earliest animal communities found during the Ediacaran Period ~565 million years ago, is unknown. In this study we analyse six of the largest and most diverse fossil assemblages from Newfoundland, Canada and Charnwood Forest, UK, using spatial point processes analyses to determine the relative influence of habitat processes (niche) and dispersal processes (neutral) on the spatial distribution of taxa. The vast majority of Ediacaran taxon distributions were controlled by neutral processes, in striking contrast to niche-dominated modern marine ecosystems, but consistent with model predictions of when neutral dynamics dominate communities. Thus the underlying processes determining metazoan community assembly have been in place since the appearance of the first macroscopic, complex animals.

Two opposing theories lie at the centre of debate regarding the fundamental dynamics that govern ecosystem structure and biodiversity: niche and neutral. Niche theory is a central tenet of classical ecological theory, whereby species avoid competitive exclusion by occupying different niches within the ecosystem (MacArthur 1984). The smaller the niche overlap, the less competition occurs between taxa, allowing more taxa to exist in an area without driving each other to extinction. Species are able to co-exist because they are different. Niche models describe selection-dominated ecosystems, whereby species dynamics operate deterministically as a series of inter-specific interactions, which act as stabilizing mechanisms for the ecosystem (Adler et al. 2007).

Neutral processes are often referred to as the null model of niche processes: instead of species *differences* enabling co-existence, their *similarity* drives high diversity (Hubbell 2001). Within neutral models, species fitness is constant, and so different taxa can co-exist because none has a significant competitive advantage over the other. Despite this seemingly highly unrealistic assumption, neutral theories have been able to accurately reproduce certain species-area-distributions (SADs; Hubbell 2001); sometimes better than niche theories; (MacArthur 1984), as well as SAD and beta diversity patterns (Condit et al. 2002, Chisholm et al. 2010).

Unified or continuous theories, whereby niche and neutral processes combine to generate species coexistence (Grave et al. 2004, Adler et al. 2007), have emerged in recent years. In these combined models, species can exhibit strong differences and strong stabilizations (niche-type), or weak stabilizations because of similar fitness (neutral-type), with classic niche and neutral models the extreme endmembers of this continuum model. However, it is often not possible to analytically determine whether the niche or neutral model fits the data

better, making it hard to untangle the relative influence of niche and neutral-type processes within modern complex ecosystems.

In order to investigate whether niche or neutral processes were the most important during the first establishment of modern-style ecosystems, we focus on some of the oldest known total-group metazoan communities: those comprising the Ediacaran macrobiota, dated to ~571-560 million years in age (Droser et al., 2017). The evolution of macroscopic metazoans was coupled with a transformation in ecosystem dynamics. Paleocommunities evolved from the assumed simple community structure of pre-Ediacaran microbial populations (Butterfield 2007), through the Ediacaran paleocommunities that exhibited both simple and complex community structures (Darroch et al. 2018), and on into the Cambrian 'modern' metazoan ecosystems with a similar ecosystem structure to the present (Dunne et al. 2008).

The oldest metazoan-dominated communities form part of the Avalonian Assemblage of the Ediacara Biota (Waggoner 2003), and are known primarily from Newfoundland, Canada and Leicestershire, UK. Avalonian soft-bodied organisms were preserved in-situ in deep-water strata dated to ~572-560 Ma (Pu et al. 2016, Noble et al. 2016), beneath volcanic ash-rich event beds (Wood et al. 2003, Narbonne 2005). As such, exposed bedding-plane surfaces preserve near-complete censuses of the communities (Wood et al. 2003, Clapham et al. 2003); though the impact of erosion of these surfaces needs to be taken into account (Matthews et al. 2017), cf. Mitchell et al. 2015). Since they were soft bodied, dead organisms could not accumulate over long time periods, removing problems associated with time-averaging of the paleocommunity. Furthermore, Avalonian ecosystems pre-date macro-predation and vertical burrowing, such that upon death, organisms were not eaten and remained in place. As a result, and because the organisms are considered to have been non-

mobile, each individual bedding plane is interpreted to record organisms that lived contemporaneously, with recently deceased and decaying organisms being the primary recognised record of identifiable time-averaging (Liu et al. 2011; Mitchell and Butterfield 2018; see also Wilby et al. 2015).

Consequently, the position and size of each fossil specimen can be interpreted to capture the life history of the organism (i.e. the dispersal, habitat and community interactions it was subject to in life). As a result, population studies using spatial point process analyses (SPPA) can infer the most likely underlying ecological and biological processes recorded within the spatial distributions of the fossils (Illian et al. 2008). For sessile organisms, community-scale spatial distributions depend on the interplay of a limited number of different factors: physical environment, which manifests as habitat associations of a taxon or taxon-pairs (Wiegand et al. 2007), organism dispersal/reproduction (Seidler and Plotkin 2006), competition for resources (Getzin et al. 2006), facilitation between taxa (Lingua et al. 2008), and differential mortality (Getzin et al. 2008).

To assess the relative influence of niche and neutral processes for these sessile communities, niche processes are identified as intra- or inter-specific habitat associations, and/or intra- and inter-specific competition (Lin et al. 2011). Density-dependent competition typically generates a segregated spatial distribution which, when broken down into taxon population size-classes, exhibits segregated largest specimens, and either random or aggregated distributions of small specimens (Diggle 2013). Such segregation is intra-specific for univariate distributions, and inter-specific for bivariate distributions, between two taxa. Neutral processes are identified where univariate distributions exhibit complete spatial randomness (CSR), and by dispersal processes that are independent of local environment (i.e.

habitat heterogeneities; Gunatilleke et al. 2006; Comita et al. 2007; Wiegand et al. 2007a; Lin et al. 2011). Intra-specific habitat associations are best-modelled as a heterogeneous Poisson model (HP), or when combined with dispersal-limitations, ITC (Harms et al. 2001; Lin et al. 2011) and inter-specific habitat associations are best modelled by a shared parents models (SPM). Dispersal patterns are indicated by a best-fit model of a Thomas Cluster (TC) or Double Thomas Cluster (DTC) model (Lin et al. 2011). Where dispersal processes are coupled to a habitat association, this process is best modelled by a Thomas cluster model combined with an inhomogeneous Poisson model (ITC; Lin et al. 2011). Therefore, for univariate distributions, neutral processes are indicated by CSR and HP, and niche processes by segregation and HP and ITC models (Fig. 2). CSR is considered a neutral process because there are no biologically or ecologically significant intrinsic or extrinsic influences on the spatial distribution. TC and DTC aggregations are also considered neutral since they describe dispersal processes, whereby aggregations arise from propagules only traveling a limited distance (thus being unable to reach all suitable substrates regardless of underlying habitat heterogeneities or species requirements; Hubbell et al. 1999; Harms et al. 2001; Seidler and Plotkin 2006). Species associations with habitat heterogeneities lead to spatial aggregations (or segregations) corresponding to the underlying habitat variations on which the species depend. Density-dependent competition, as indicated by size-dependent spatial segregation (Kenkel 1988), indicates a lack of sufficient resources, and is therefore also a niche-based process.

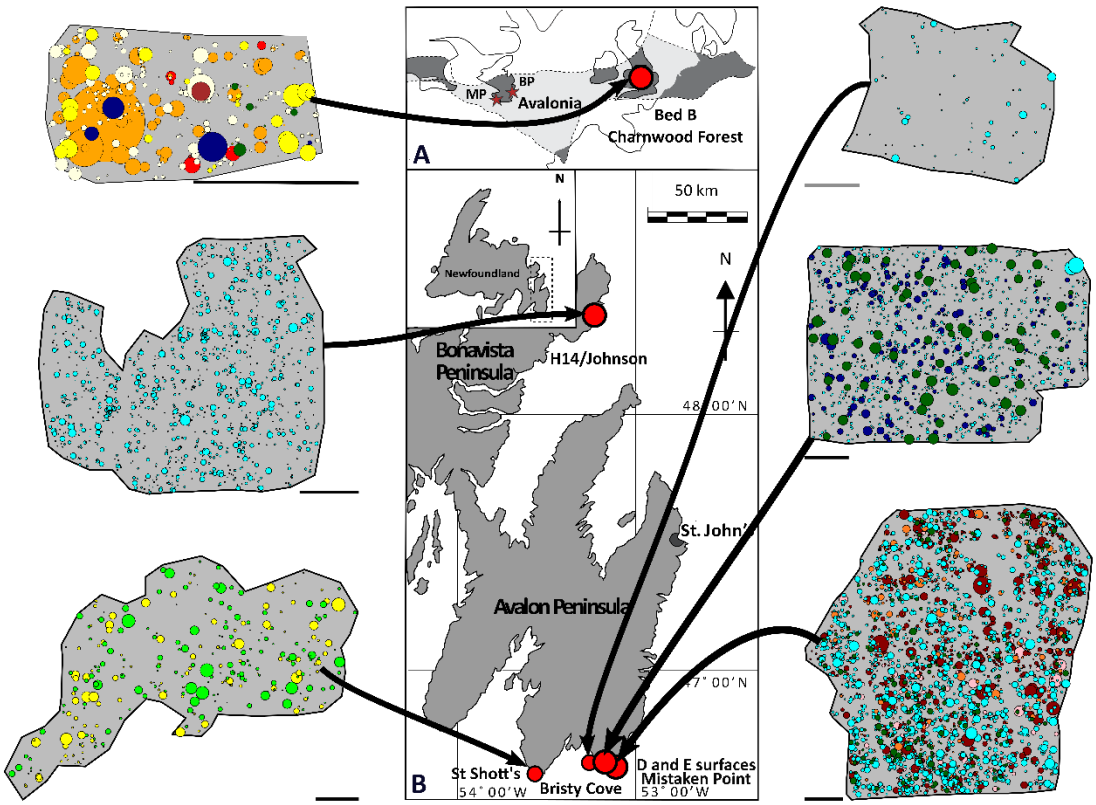

Figure 1: Locality Map of study sites, showing: A, the relative location of sites within the micro-continent of Avalonia. B, the Newfoundland sites of the Bristy Cove (BR5), 'D' and 'E' surface, Mistaken Point Ecological Reserve, the St Shott's (Sword Point) surface, and the H14/Johnson surface, Bonavista Peninsula (modified from Liu 2016). Associated spatial maps for each locality show the positions of the fossil specimens (indicated by a circle). Black scale bar = 1m, grey scale bar = 0.1m. Different colors indicate different taxa as follows: Thectardis *navy;* Fractofusus *light blue;* Charnia *bright yellow;* Charniodiscus *dark red*; Aspidella *light green;* Bradgatia *dark green ; Feather Dusters light orange;* Primocandalebrum *dark orange;* Trepassia *dark purple;* Beothukis *bright pink;* Pectinifrons *dark blue; Brushes brown;* Avalofractus *navy;* Hylaecullulus *light yellow.*

In this study we assessed the univariate and bivariate spatial distributions of taxa from six Avalonian communities: the 'D', 'E' and Bristy Cove surfaces in the Mistaken Point

Ecological Reserve; the St Shott's surface at Sword Point; the H14 (Johnson) surface at Little Catalina in Newfoundland, Canada; and Bed B, Charnwood Forest, UK. We mapped the bedding-plane assemblages of fossils at a coarse scale using LiDAR, and then captured the fine-scale fossil details using photogrammetry and high-resolution laser scanning (SI Methods). Combination of these datasets enabled full maps of the paleocommunities to be reconstructed (Fig 1).

For each surface, we tested for erosional biases and tectonic deformation, taking these factors into account if they were considered to have significantly affected specimen density distributions (SI Methods). Non-abundant taxa (< 30 specimens) and taphomorphs (such as organ taxa or the decaying and/or poorly preserved remains of carcasses, ivesheadiomorphs) were excluded from analyses, leaving 10 abundant taxa (see SI Methods for full taxonomic descriptions), of which three (*Charniodiscus*, *Charnia*, *Bradgatia*) are found on two bedding planes and one (*Fractofusus*) on four bedding planes. The univariate spatial distributions of each taxon on individual bedding planes were described using pair correlation functions (PCFs). A PCF = 1 indicates a distribution that was completely spatially random (CSR); PCF > 1 indicates aggregation; and PCF < 1 indicates segregation (Diggle 2003, 2015; Illian et al. 2008). Monte Carlo simulations and Diggle's goodness-of-fit tests (p_d) were used to indicate significantly non-CSR distributions where the observed PCF deviated outside the simulation envelope and $p_d \ll 1$ (Diggle 2013). Where a non-CSR distribution was observed, HP, TC and ITC models were fit to the data, with the highest p_d value indicating the best-fit model (Fig. 2). Identifying the processes behind spatial patterns is not straightforward (Levin 1992; Murrell and Law 2003; Wiegand et al. 2007; McIntier and Fajardo 2009; Wiegand and Moloney 2013), but the best-fit model is interpreted to indicate the most likely underlying processes, with CSR and TC reflecting neutral processes and HP and ITC reflecting niche

processes (Lin et al. 2011). Bivariate distributions were assessed to ascertain inter-specific interactions and associations between taxa (cf. Mitchell and Butterfield 2018). Niche processes are bivariate habitat associations indicated by shared parents models (SP) and density-dependent competition. Density-dependent competition has the spatial signature of a segregated distribution, which, when broken down into PCFs of size-classes, has segregated largest specimens and either CSR or aggregated small specimens (Diggle 2013).

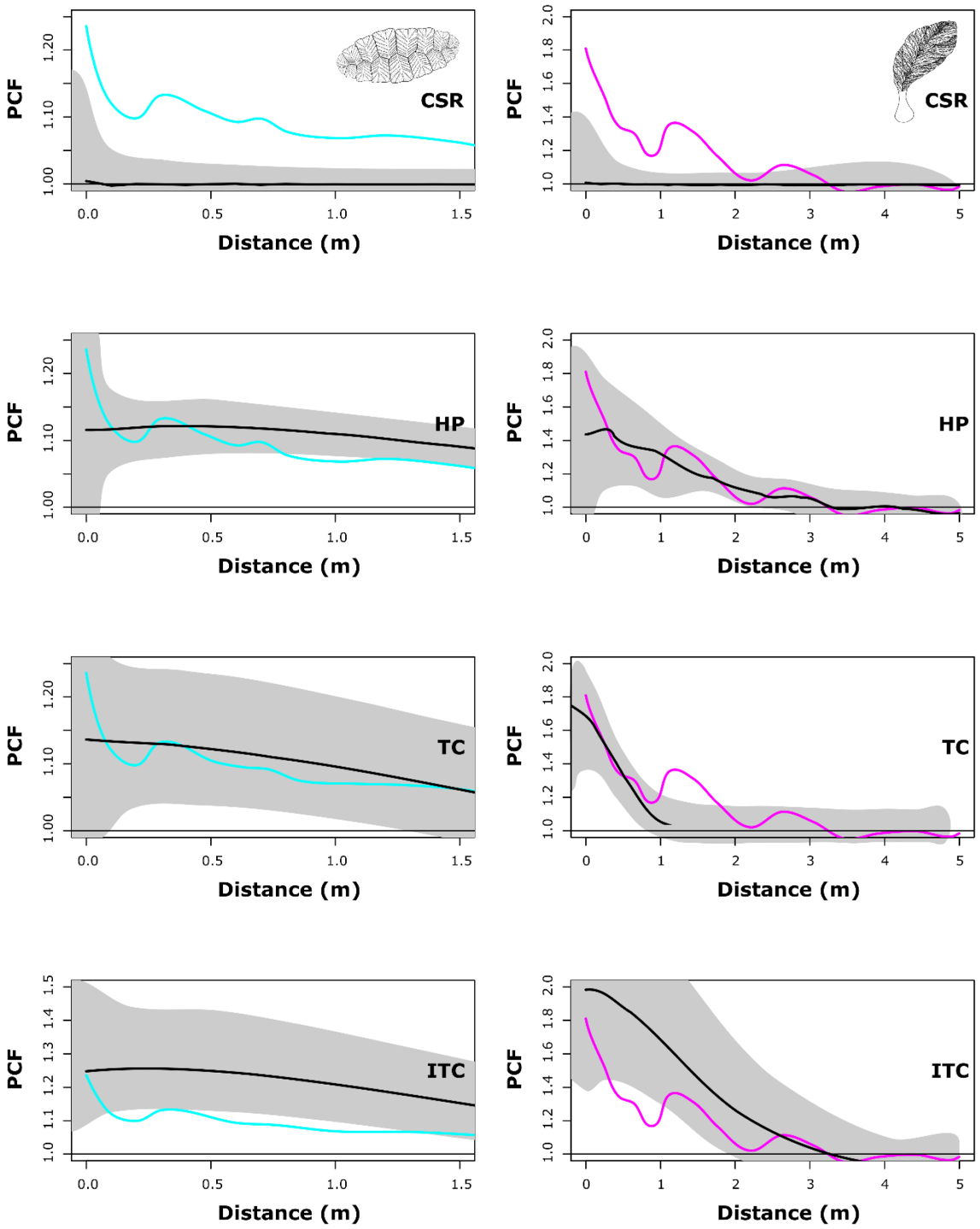

Figure 2. Univariate PCF for 'D' surface Fractofusus *and 'E' surface* Beothukis *under four different spatial models: CSR, HP, DTC, ITC. The model lines are dashed, the solid lines are the observed spatial distributions and the grey area represents the simulation envelope of 999 Monte Carlo simulations.*

Results and Discussion

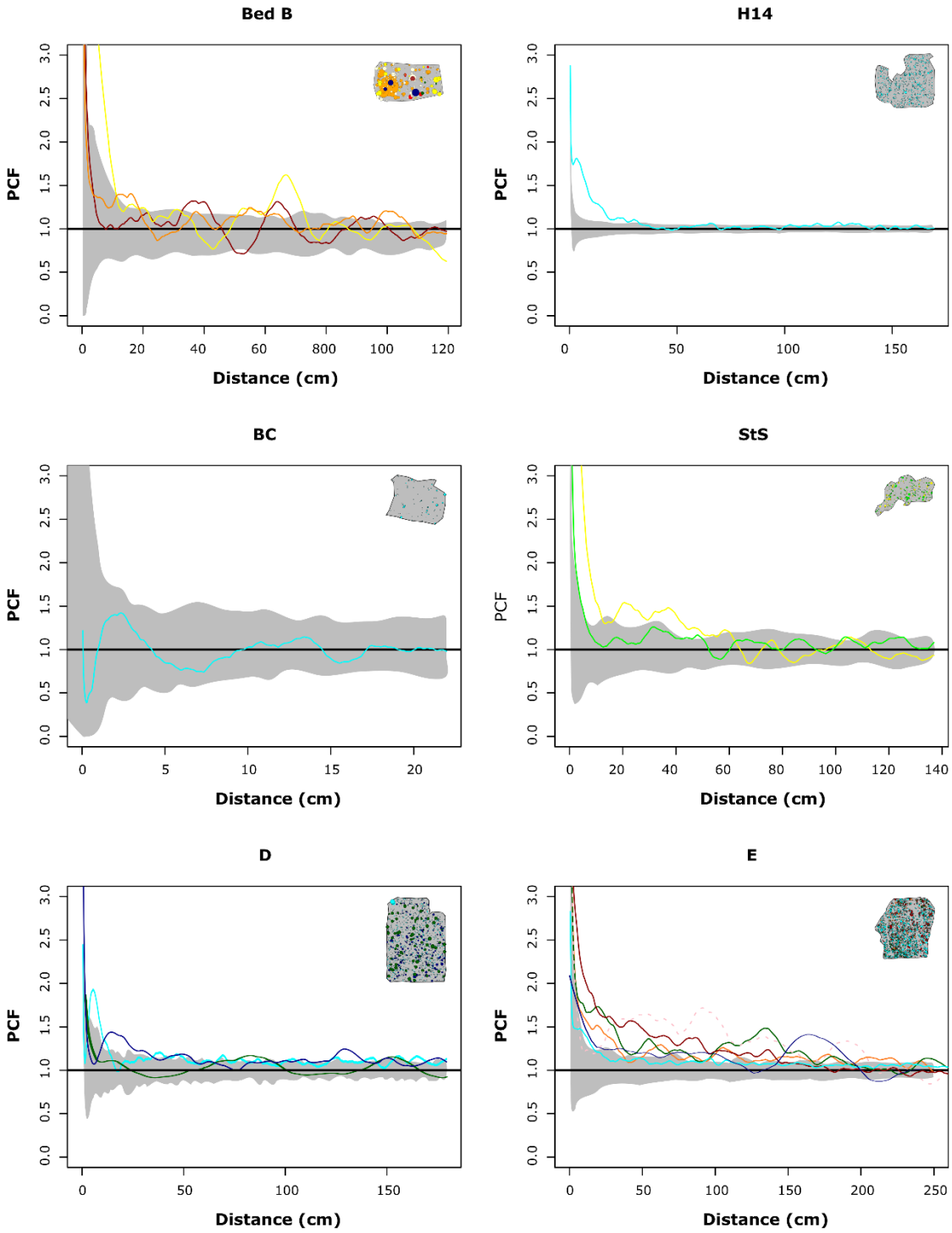

Figure 3 Univariate PCF for surfaces A) 'E' surface, B) 'D' surface, C) Bristy Cove, D) St. Shott's, E) H14/Johnson and F) Bed B. Where a niche model is the best-fit model for the distribution, it is drawn as a dashed line. Neutral models are drawn as solid lines. Different

colors indicate different taxa as follows: Thectardis *navy;* Fractofusus *light blue;* Charnia *bright yellow;* Charniodiscus *dark red;* Aspidella *light green;* Bradgatia *dark green; 'Feather Duster', light orange;* Primocandalebrum *dark orange;* Trepassia *dark purple;* Beothukis *bright pink;* Pectinifrons *dark blue; Brushes brown;* Avalofractus *navy;* Hylaecullulus *light yellow.*

	CSR	HP	TC/DTC	ITC
BED B	0.00%	0.00%	100.00%	0.00%
H14/JOHNSON	0.00%	0.00%	100.00%	0.00%
ST SHOTTS	50.00%	0.00%	50.00%	0.00%
BRISTY COVE	100.00%	0.00%	0.00%	0.00%
D SURFACE	66.67%	0.00%	33.33%	0.00%
E SURFACE	16.67%	16.67%	66.67%	0.00%

Table 1. Proportion of best-fit univariate models by surface, showing the percentage of taxa with univariate spatial distributions that are best described by CSR, HP, TC (or DTC) and ITC models.

Across the six surfaces and the 16 taxon univariate distributions examined, 5 taxon distributions were best modelled by CSR (Fig. 3, Table 1. SI Table 2). Of the non-CSR taxa distributions 10 were best modelled by TC (or DTC). No taxa were best modelled by ITC models (Table 1). Only *Beothukis* on the 'E' surface had a HP best-fit model univariate spatial distribution (Fig. 2, Table 1). None of the 16 univariate taxon distributions exhibited intra-specific spatial segregation, meaning there is no evidence of intra-specific competition. Our results reveal only one univariate taxon distribution ('E' surface *Beothukis*) that was best-modelled by a niche process.

The studied paleocommunities only have spatial scales in the order of decameters. However, by comparing the univariate spatial distributions of the same taxa found at different sites representing communities separated by large spatial and temporal scales, we can gain some indication of whether taxa behave differently over large-spatial scales. Four taxa are abundant across multiple bedding planes (*Bradgatia*, *Charnia*, *Charniodiscus* and *Fractofusus*), and these taxa all exhibit the same type of best-fit model (CSR, TC, TC and TC/DTC) on all the surfaces**.** Previous work has demonstrated how *Fractofusus* shows the same consistent spatial distributions across multiple surfaces (Mitchell et al. 2015) in different geological formations (potentially indicating different environments and ages; cf. H14 and 'E' surface). *Bradgatia*, *Charnia* and *Charniodiscus* also show consistent spatial distributions (Fig. 3), even when the taxa inhabit ecosystems originally located in different basins (e.g. *Charniodiscus* from the 'E' surface and Bed B) and separated by ~6 million years (Noble et al. 2015, Pu et al. 2016). The consistency of these results suggests that the small-spatial scale ecological behaviour of these taxa did not change over large spatial and temporal scales.

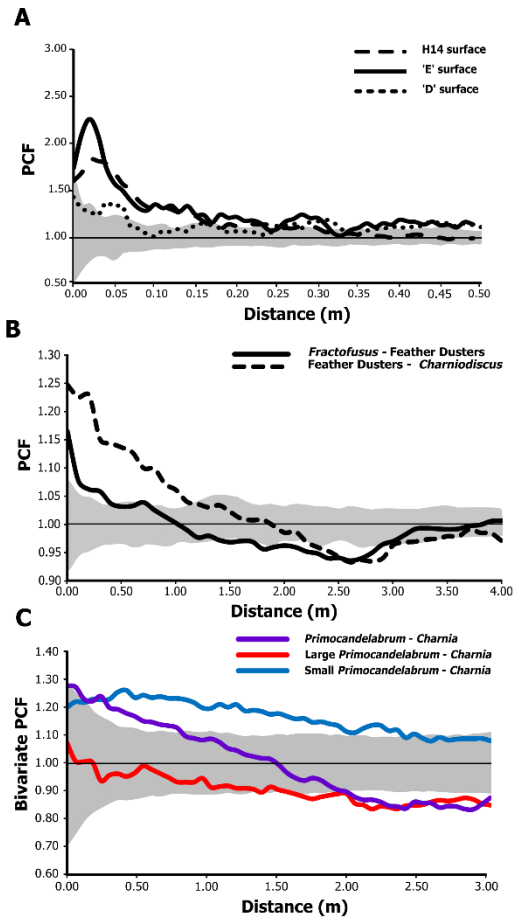

Figure 4: Multi-surface univariate PCFs of A) Fractofusus *(from Mitchell et al. 2015). B) Non-CSR bivariate distributions of the 'E' surface (from Mitchell and Butterfield 2018) and C) the non-CSR bivariate distributions Bed B, Charnwood Forest and). The x-axis is the inter-point distance between organisms in metres. On the y-axis, PCF=1 indicates complete spatial randomness (CSR), <1 indicates segregation, and >1 indicates aggregation.*

Of the four communities with more than one abundant (> 30 specimens) taxon present, two surfaces exhibited only CSR bivariate distributions ('D' surface (Mitchell and Butterfield 2018) and St Shotts). The 'E' surface (Mitchell and Butterfield 2018) and Bed B exhibit non-CSR bivariate distributions (Fig 3). The three non-CSR bivariate distributions on Bed B indicate shared habitat associations (Fig 4c, SI Table 1) as do the three bivariate distributions on the 'E' surface (Mitchell and Butterfield 2018, Mitchell and Kenchington 2018). Habitat

associations are niche processes (Lin et al. 2011), thus these results demonstrate that both niche and neutral processes operated within these communities. These bivariate associations are much weaker in PCF magnitude than the univariate distributions (Figs 3 and 4), showing that niche processes had less impact on spatial distributions than neutral processes. Furthermore, competition is rare, and is also relatively weak in magnitude when observed (Fig 4b,c, Mitchell and Butterfield 2018, Mitchell and Kenchington 2018). These results demonstrate that environmental associations had a relatively small impact on the community structure of these Ediacaran communities. On the 'E' surface, segregations reduced specimen density by 25%, and aggregations increased taxon density by 56% (Fig. 4). In contrast, intra-specific aggregations are large, reflecting an increase in taxon density of 250–600%. The two habitat associations on the 'E' surface (Feather Dusters–*Fractofusus* and Feather Dusters–*Charniodiscus*) exhibited small scale specimen aggregations (increase of 34% under 0.2m and 56% under 1.2m respectively) with large scale reduction in specimen density (11% over 1m and 13% over 2.1m respectively). Similarly on Bed B, habitat association between *Charnia* and *Primocandelabum* increased taxon density by 87%, whereas segregations reduced taxon density by 10%. Univariate dispersal-generated aggregations increased taxon density by 180–500% (Figs 3 and 4). These results demonstrate that habitat associations were present in some paleocommunties, but had a relatively small impact on organism distributions.

Our results support combined theories of community assembly whereby niche and neutral theories are not mutually exclusive; they act along a continuum or spectrum, with differing extents of niche and neutral processes present in different circumstances (Gravel et al. 2006; Fisher and Mehta 2014). The dominance of univariate niche best-fit models, repetition of best-fit univariate models across different communities, and the rarity and weakness of

bivariate niche best-fit models, all combine to provide strong evidence that neutral processes dominated Avalonian communities, with only limited niche-based influence. These neutral-dominated community dynamics contrast with those observed in the modern marine realm, where neutral models do not provide good descriptions of the community dynamics (Dornelas et al. 2006, Connolly et al. 2014).

The striking difference in dominance of niche versus neutral processes raises the intriguing question as to whether the community dynamics of these oldest known macroscopic animal communities had fundamentally different dynamics to the present. Previous work on the balance of niche–neutral influences on community assemblage in Quaternary fossil assemblages provides strong model and empirical support for environment-led models of assembly (Jackson and Blois 2015). However, Avalonian communities appear to differ from the majority of existing marine systems in that the maximum number of generations currently documented for these Avalonian paleocommunities is three generations (Mitchell et al. 2015), though some communities show rare survivors (Wilby et al. 2015) or evidence of secondary community succession (Liu et al., 2012). These population structures suggest that the preserved paleocommunities are not always mature, being culled prematurely by the frequent event beds that killed and preserved them, limiting their maturity (Wilby et al. 2015). Frequent sedimentary disturbances could also explain why there is limited intra-specific competition, with the lack of intra-specific competition demonstrating that populations did not reach their carrying capacities. Recent models show that community dynamics in small populations in fluctuating environments are dominated by neutral processes (Fisher and Mehta 2014).

While some Avalonian taxa were global, with wide dispersal ranges (indicated here by CSR), the majority of the specimens within each community consisted of taxa with limited dispersal ranges on the order of decimetres (Mitchell et al. 2015. Mitchell and Kenchington 2018). Such limited dispersal range have been shown to decrease ecological selection and decrease effective community size, while increasing the dominance of neutral-processes (Ron et al. 2018). Therefore, while the dominance of neutral-based processes within these paleocommunities differs significantly to the modern marine realm, the underlying dynamics can still be described by established models of community dynamics. Therefore, we propose that the oldest known macroscopic metazoan paleocommunities operated under different processes to the present, but that underlying dynamics of community assembly have existed unchanged over the last ~570 million years.

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