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Competition in the deep sea: phylogeny determines destructive impact of wood-boring xylophagaids (Mollusca: Bivalvia)

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Abstract

How biotic interactions contribute to structuring deep-sea communities remains poorly known. An example of exploitation competition, in which over time one species dominates a habitat to preclude its use by competitors, is highlighted here. Sunken wood is the obligate habitat of deep-sea wood borers of the Xylophagaidae Purchon, 1941 which eat wood and, with symbiotic bacteria, digest it. Enigmatically, some wood falls remain robust despite xylophagaid boring. Xylophagaids bore other wood falls so heavily that they crumble after just a few months. We perform a meta-analysis of experimental wood deployments and view the results from a phylogenetic perspective. Of 15 deployments recovered after 5 to 25 months from 200 to 3232 m deep, seven were so heavily bored to be crushable by hand. Eight were bored but remained robust. The groups did not significantly differ in wood size, type, temperature, depth, or duration. Members of the *Xylophaga dorsalis* (Turton, 1819) clade, reported in two studies to recruit and bore faster than confamilials, bored all seven crushable deployments; seven of the eight intact deployments were bored by other xylophagaids. Fecal chimneys line and thus narrow the boreholes of this clade; fluid flow is impeded, a clear liability. The lignin-rich fecal chimneys may, however, cue larval settlement and at resultant high population densities, lower oxygen availability. Members of the *X. dorsalis* clade, being hypoxia-tolerant, thrive but other xylophagaids appear to suffer, perhaps due to interference competition. The shared derived characters that unite this clade allow them to exploit low-oxygen wood that is intolerable for competitors.

Keywords Exploitation competition · Ecosystem engineer · *Xylophaga dorsalis* · Importance of phylogeny

Introduction

Competitive interactions in the deep sea remain little-known but are likely to be important in structuring communities. We present a study that reveals, we argue, exploitation competition, in which individuals of one species monopolize limiting resources. Our focus is on sunken wood that forms deep-sea

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wood falls. Although ephemeral and stochastically distributed, wood falls can sustain high levels of alpha biodiversity if colonized by obligate wood-boring bivalves of the Xylophagaidae Purchon, 1941, with seven named genera and about 61 named species.

Xylophagaids bore into wood and generate slightly elongate, non-overlapping boreholes that differ subtly by species (Amon et al. 2015a). They eat the wood they remove, digesting cellulose with the aid of symbiotic bacteria, which also fix nitrogen (Distel and Roberts 1997). These actions sustain biodiversity on deep-sea wood falls, in some cases over years (e.g., McClain and Barry 2014). If xylophagaids are absent, few other animals recruit to sunken wood (Gracia et al. 2019; Young et al. 2022). Because their boreholes generate space and the animals and their bacteria convert wood into digestible food available to non-xylophages, xylophagaids have been deemed ecosystem engineers (e.g., McClain and Barry 2014; Harbour et al. 2021).

The study of deep-sea wood falls and their borers has been accelerated by the use of experimental deployments that mimic natural wood falls. Turner (1973) used these to

document the very existence of deep-sea wood borers; the deployments have since secured macrofauna and microbial specimens for study of wood fall biodiversity (Turner 1978; Sandström et al. 2005; Voight 2007; Romano et al. 2013; Yücel et al. 2013; Judge and Barry 2016; Kalenitchenko et al. 2018), and they have been used to return complete eco-systems for analysis (e.g., McClain et al. 2016). Short-term experimental deployments, however, reveal an enigma (Fig. 1). Xylophagaid-bored wood sometimes forms long-lived biodiversity hot spots, but other times, the xylophagaid borers reduce deployed wood to a minimal skeleton, crushable by hand, in as little as a few months (Haderlie 1983; Voight 2007; Romano et al. 2013; Amon et al. 2015b).

The heavy boring that results in the deployments being crushable by hand has been attributed to the proximity of unseen wood falls that serve as larval sources, to continual high larval availability, to an absence of predators, to long observation periods, to the bivalves' specialization to their ephemeral habitat, to warmer temperatures, and/or to properties of the wood (e.g., Metaxas and Kelly 2010; Amon et al. 2015a). Despite the fact that a given piece of wood is a finite resource that xylophagaids must consume to survive, biotic interactions among borers within a wood fall have been largely ignored. If one species, or a group of related species, can dominate a wood fall by means such as higher fecundity, increased larval availability, or mixotrophy, the contrast between long-lived, robust, and short-lived, heavily bored wood falls might be simply explained.

Here we use a meta-analysis including multiple xylophagaid-bored deployments from around the world to compare the taxonomic composition of borers in wood that remained largely intact to those in wood that was crushable by hand (or heavily bored) on recovery. We assign the xylophagaids removed from wood of

contrasting condition to their respective clades defined by anterior adductor cover and siphon morphology and molecular characters (Voight et al. 2019). We find members of a single clade are associated with every heavily bored deployment in our analysis. We then consider aspects of their biology that may contribute to their competitive superiority.

Material and methods

To assess the importance of taxon membership in determining the fate of wood falls, we undertook a two-part study. First we performed a meta-analysis based on literature reports of experimental wood deployments, including ten deployments from the northeast Pacific, two from both the Indian Ocean and Mediterranean Sea, and one from a Norwegian fjord; the depths are from 200 to 3232 m. Inclusion of diverse datasets is among the primary advantages of a meta-analysis, especially given the costs of deep-sea research. Other advantages are that the increased sample size allows more powerful statistical analyses and that the odds of a given random event impacting every study included and generating a bias are greatly reduced; the deployments considered here were made from 1979 to 2017, during 7 months of the year. We excluded deployments less than 2 cm in smallest dimension as overly vulnerable.

Deployments considered to be heavily bored were those the authors reported were crushable by hand at recovery. Deployments considered to be largely intact were those the authors noted to be solid or intact or to require use of a hammer and chisel to sample the xylophagaids. We quote the published description of the recovered wood in Table 1 with the page reference; we also re-examined the preserved wood (deposited at the Field Museum collections) from which the

Fig. 1 Two deployments of Douglas fir recovered after 24 months at depth **a** from 2701 m depth, bored by *Xylonora corona* (Voight, 2007). The distance from the top to the bottom of the wood is 10.16 cm; **b** from 2211 m depth bored by *Xylophaga oregona* Bartsch, 1921, a member of the *X. dorsalis* (Turton, 1819) clade (from Voight 2007)
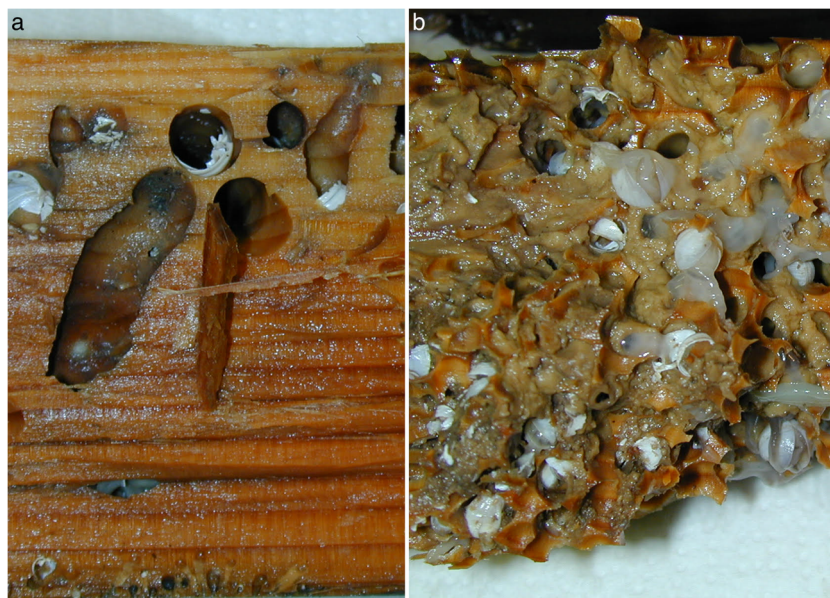
Table 1 Recovered wood deployments listed by their condition at recovery with the dominant xylophagaid borer, locality, depth, sea temperature, soft or hardwood, deployment month year, and duration in months, size, and surface area, condition when recovered and reference. At the end of each section are the W statistics and probability from the Mann-Whitney U test between the groups for each variable. Months are numbered with the summer solstice month being 1. An asterisk after the species name indicates JRV verified the species determination

Taxon	Ocean, lat long	Depth (m)	°C	Soft or hard wood	Deployed mo yr/ duration	Size cm (kg)/area cm³	Recovery condition	Reference
Xylophaga s.l. murrayi Knudsen, 1967	SW Indian 41° 22S 42° 55E	732	4.3	Mango (hard) green	Dec 2009/23.5	2.15; 4.5; 5.3; 6.15 kg	Very solid	Amon et al. 2015b (p. 6)
Xylonora corona (Voight, 2007)*	NE Pacific 42° 45N 126° 42W	2701	2	Fir (soft) green	July 2002/25	47.5 × 10 × 10/4750	Largely intact	Voight 2007 (p. 389)
Xylophaga s.l. microchira Voight, 2007*	NE Pacific 47° 43N 127° 48W	2639	2	Fir (soft) green	Sept 2002/10	47.5 × 10 × 10/4750	Intact	Voight 2007 (unpub.)
Xylophaga s.l. microchira*	NE Pacific 47° 57N 129° 6W	2211	2	Fir (soft) green	Sept 2002/10	47.5 × 10 × 10/4750	Intact	Voight 2007 (unpub.)
Xylophaga dorsalis Turton, 1819	Norway fjord 60.7° N 5,4° E	530	8	Pinus sp. (soft) Untreated	May 2017/10	15 × 15 × 15/3375	Borers extracted with hammer/chisel	Harbour et al. 2021
Abditoconus heterosiphon (Voight, 2007)*	NE Pacific 47° 47N 127° 42W	2656	2	Fir (soft) green	Sept 2002/10	47.5 × 10 × 10/4750	Intact	Voight 2007 (unpub.)
Xylonora zierenbergi (Voight, 2007)*	NE Pacific 47° 16N 127° 36W	2666	1.8 ± 0.03	Fir (soft) untreated	Apr 2013/14.5	18.3 × 19 × 8.8/3060	"Largely intact"	Young et al. 2022
Xylonora zierenbergi*	NE Pacific 41° 0N 127° 30W	3232	2	Fir (soft) green	July 2002/25	47.5 × 10 × 10/4750	Intact	Voight 2007 (unpub.)
Range/median	**41 to 61/47**	**520 to 3232/2639**	**2 to 8/2**		**1 to 11/3 10 to 25/12.25**	**3060–4750/4750**		
Xylophaga dorsalis*	Medit. Sea 41° 34N 2° 54E	900	3–13.3	Fir (soft) no data	Nov 2008/9	8 × 8 × 8/512	Crumbled on handling	Romano et al. 2013 (p. 179)
Xylophaga dorsalis*	Medit. Sea 41° 31N 2° 51E	1200	3–13.3	Fir (soft) no data	Nov 2008/9	8 × 8 × 8/512	Partly crumbled	Romano et al. 2013 (pp. 178-179)
Xylophaga indica Smith, 1904	SW Indian 32° 43S 57° 16E	750	10.1	Mango (hard) green	Nov 2009/25	4.4; 4.8; 10.9 kg	Disintegrating/almost completely consumed	Amon et al. 2015b (p. 127)
Xylophaga oregona Voight, 2007*	NE Pacific 45° 56N 129° 59W	1520	2	Fir (soft) green	Sept 2002/10	47.5 × 10 × 10/4750	Crushable by hand	Voight 2007 (p. 389)
Xylophaga oregona*	NE Pacific 47° 56N 129° 6W	2211	2	Fir (soft) green	Sept 2002/24	47.5 × 10 × 10/4750	Crushable by hand	Voight 2007 (p. 389)
Xylophaga oregona*	NE Pacific 47° 57.5N 126° 2W	1596	2.5 ± 0.1	Fir (soft) untreated	Apr 2013/14.5	18.3 × 19 × 8.8/3060	Crumbling	Young et al. 2022 (p. 30)
Xylophaga washingtona Bartsch, 1921	NE Pacific 36° 39N 121° 51W	200	<10	Not specified	March 1979/4–6	10 × 10 × 20/2000	Crumbling/disintegrating	Haderlie 1983 (pp 341-342)
Range/median	**33 to 48/42°**	**200 to 2211/1200**	**2 to 10.1/8**		**3 to 11/5 5 to 25/10**	**512 to 4750/2530**		
Mann-Whitney U/p value	**38/0.262**	**43/0.082**	**11/0.051**		**15/ 0.147** **36/0.343**	**32/0.087**		

species Voight (2007) reported were removed, terming it crushable or intact (Fig. 1).

The locality, depth, temperature, wood type and treatment history, deployment month and duration, surface area, and the most common xylophagaid species that bored each of the deployments considered are reported on Table 1 with the group ranges and medians. Temperatures were reported in the original reports, although an equipment malfunction forced the 10-month deployments reported by Voight (2007) from over 2200 m to be estimated at 2°C. Because the data include Northern and Southern Hemispheres, for statistical analysis we assign 1 to the summer solstice month (July in the North, December in the South) and number other months sequentially. In two instances, deployment weights rather than surface areas were reported (Amon et al. 2015a), forcing us to calculate and compare the medians of the weights in an analysis separate from the surface area comparison. We compared environmental variables between the heavily bored and largely intact deployment groups with Mann-Whitney U tests. If temperatures were reported as a range (Romano et al. 2013), we used the mean value in the test. Test statistics and probabilities are reported in Table 1, as is whether softwood (pine or fir) or hardwood (mango) formed the deployment. These types of wood differ in their density, anatomy, and chemical composition (Pereira et al. 2003).

Xylophagaid species names cited in the original works were accepted; JRV examined specimens from the studies indicated in Table 1. Amon et al. (2015b) accessed the types at the Natural History Museum (D. Amon, pers. comm.); the species cited by Haderlie (1983) and Harbour et al. (2021) are the only xylophagaids known in their study areas. Because the genus *Xylophaga* Turton, 1822 is paraphyletic (Voight et al., 2019), species assigned to that genus but not members of the clade containing *X. dorsalis* (Turton, 1819), the type species of the genus, are indicated by "s.l."

To test whether heavily bored and largely intact deployments were bored by different species groups, we compared three groups. First was the species of *Xylophaga* s.l. and *Xylonora* Romano, 2020 in Romano et al. (2020). The calcareous mesoplax plates of these species serve as a putative synapomorphy; they are currently separated only by whether or not they have been sequenced (Romano et al. 2020). We assume they are a clade, but acknowledge they may be paraphyletic. Second, we include species of *Abditoconus* Voight, 2019, which have unusual nitrogen isotopes that are comparable to those of species of the clade of *Xylophaga dorsalis* (Voight et al. 2020). Third were species in the clade of *Xylophaga dorsalis*. In these species, the excurrent siphon is shorter than the incurrent siphon; it opens and thus releases most fecal pellets, inside the borehole. The pellets are compacted and accumulate around the siphon, typically extending beyond the wood-water interface to form a "chimney" (Purchon, 1941; Turner, 2002; Romano et al. 2014). The clade

includes, among others, *X. oregona* Voight, 2007; *X. washingtona* Bartsch, 1921; and *X. indica* E. A. Smith, 1904, following Turner (2002). We tested whether the above three groups were more frequent in the heavily bored compared to the largely intact deployments using Fisher's exact test. We also compiled published rates of boring and population densities of xylophagaids, focusing on heavily boring taxa.

The second part of our study considers characters shared among heavily boring xylophagaids to assess whether these characters may contribute to their more aggressive boring. Although Voight et al. (2020) found no isotopic evidence of chemosynthetic input in xylophagaids, chemosynthetic bacteria could occur in the borehole, where sulfide is hypothesized to be oxidized (Kalenitchenko et al. 2018). If so, precipitated elements such as sulfur or calcium should be abundant in the borehole and especially in the fecal chimney. A chemical microanalysis with an Oxford Instruments XMax50 Energy Dispersive X-ray Spectroscopy (EDS) system attached to a Zeiss Evo 60 scanning electron microscope tested this prediction. To reveal their elemental composition, we analyzed fecal chimneys of *X. dorsalis* that had been preserved in ethanol after having been removed 6 months before from a wild wood fall that also had bacterial mats and pogonophoran tubes; we also analyzed fecal chimneys of *X. oregona* that had been preserved in situ in the wood of Douglas fir for 10 years. Considering the chimneys of two species allowed us to assess the generality of our results, despite the more anoxic substrate of the *X. dorsalis*. Micro-Raman spectroscopy with a WITec alpha 300R 532 nm laser Raman system was applied to the chimneys to confirm results. The chimneys had been longitudinally split and air-dried for at least 72 h prior to analysis.

Results

Our meta-analysis revealed that crushable deployments were significantly more often bored by species of the clade of *Xylophaga dorsalis* than were the intact deployments ($p = 0.048$). Of 15 deployments analyzed, seven were crushable by hand, all of which were bored by members of the *Xylophaga dorsalis* clade; seven of the eight intact deployments were bored by members of other xylophagaid clades. Mann-Whitney U tests found no significant differences in the environmental and deployment variables considered between the groups (Table 1), although temperature very nearly significantly differed ($p = 0.0505$). Most deployments in both groups were composed of softwoods; each group had one hardwood. Haderlie (1983) did not specify the wood deployed. All wood for which treatment history was reported was either green or untreated (Table 1). Amon et al.'s (2015b) deployments had essentially equal median weights (4.8 and 4.9 kg).

The second part of our analysis focused on the fecal chimney, a character that unites the heavily boring members of the *X. dorsalis* clade. The chimney lines the borehole and extends beyond the wood-water interface. The inner lining of longitudinally sectioned, air-dried fecal chimneys had a distinct sheen, consistent with Purchon's (1941) report of a mucus lining. Our EDS analyses found organic matter composed over 90% of the fecal chimneys of *X. dorsalis* and *X. oregona* (Fig. 1); major components of seawater were also abundant (Table 2, full data in Online Resource Table 1). The fecal chimney of *X. dorsalis* had considerably more sulfur, a major component of seawater, than did that of *X. oregona*, consistent with the evidence noted above that the wood of the former had previously supported chemosynthetic animals. The inner chimney of *X. oregona* had less sulfur than did the outer (Table 2).

Raman spectroscopy revealed the major components of the *X. dorsalis* chimney to be lignin, cellulose, and hemicellulose, specifically xylan (Fig. 2). It also identified the white spots on the siphon of *X. dorsalis* as calcite and the shell's beak and mesoplax to be aragonite (Online Resource Table 2).

Discussion

Among the reports considered here, regardless of deployment location, depth, temperature, or wood size or type, only members of the *Xylophaga dorsalis* clade bored wood so heavily that it could be crushed by hand; wood bored by other xylophagaids for the same duration remained largely intact. Although we do not assert that this pattern is invariant, no longer are ad hoc explanations, such as the proximity of an unseen larval source, required to explain heavily bored wood falls. Two reports that did not meet our minimal size deserve mention. A 20 × 8 × 2 cm deployment bored by *Xylonora atlantica* (Richards, 1942) crumbled after 8 to 10 months at 100 m depth in 17.5° C (Romey et al. 1994); *Xylophaga*

washingtona bored a comparable 22.8 × 10 × 1.9 cm deployment at 200 m depth until it was spongy (with 255 boreholes/cm^2) after 2.4 months at 7°C (Tipper 1968; temperature estimated from Meseca 1967). Because *X. washingtona*, a member of the *X. dorsalis* clade, bored for a shorter time in colder temperatures, these observations support the hypothesis of heavy boring by members of that clade. The one reported deployment that was bored by *X. dorsalis* but was not crushable by hand "would have degraded to the point of collapse" if it had spent longer than 10 months on the bottom (Harbour et al. 2021, p. 87).

Incomplete knowledge of the xylophagaids cautions us against making absolute statements, but available data indicate that the clade of *X. dorsalis* is exceptional. Member species of the *X. dorsalis* clade, termed Groups 5 and 6 by Turner (2002) and Voight (2008), have a pooled depth range of 10 to 4626 m, overlapping with but on average significantly shallower than that of other xylophagaids (Voight 2008). Their elevated nitrogen isotopic values are consistent with opportunistic filter feeding (Voight et al. 2020). The species *X. dorsalis* (as *Xylophaga* sp. A) recruits in greater numbers, and grows faster than do the xylophagaids *Abditoconus brava* (Romano, Pérez-Portela & Martin, 2014 in Romano et al. 2014) reported as *Xylophaga* sp. B by Romano et al. (2013) and *Xylonora atlantica* reported by Romey et al. (1994). *Xylophaga indica* of the same clade (following Turner 2002) recruits faster and grows slightly faster than does *X.* s. l. *murrayi* Knudsen, 1967 in comparable deployments; these differences were attributed to warmer temperatures (4.3 versus 10.1°C), differences in predation, and/or larval supply that affected population densities (Amon et al. 2015b). Using a micro-CT scans, Amon et al. (2015a) calculated that *Xylophaga depalmai* Turner, 2002 and *X. indica*, members of the *X. dorsalis* clade, bore more (0.438 to 0.606 cm^3/year) than does *X.* s. l. *murrayi* (0.235 cm^3/year). We suggest phylogeny plays a significant role, but the lack of data concerning fecundity and the timing of larval competence from across the

Table 2 Elemental analysis in mean %weight ± relative 10% (2σ) of fecal chimneys of *Xylophaga dorsalis* and *X. oregona* (inner and outer). Major components of seawater (*) and clay (**) indicated

Element	*X. dorsalis*, n =10	*X. oregona* inner, n = 7	*X. oregona* outer, n = 4
C	58.7 ± 12.1	65.9 ± 20.6	60.6 ± 8.5
O	31.7 ± 8.7	32.8 ± 20.2	34.8 ± 11.9
C+O	90.4 ± 5.7	98.7 ± 1.4	95.4 ± 3.5
Cl*	1.8 ± 1.1	<0.1 ± 0.04	0.1 ± 0.2
Na*	2.0 ± 0.6	0.2 ± 0.1	0.3 ± 0.3
S*	2.3 ± 2.0	0.2 ± 0.2	0.5 ± 0.9
Mg*	0.5 ± 0.3	0.2 ± 0.1	0.2 ± 0.3
Ca*	1.4 ± 3.0	0.4 ± 0.7	1.9 ± 2.8
K*	0.1 ± 0.2	<0.1 ± 0.04	<0.1 ± 0.04
Si**	0.2 ± 0.3	0.2 ± 0.3	0.1 ± 0.07
Other	Cu 1.0 ± 0.8	Al** 0.1 ± 0.1; Fe 0.1 ± 0.2	Fe 0.5 ± 1.0

Fig 2 Typical Raman spectra on fecal matter of *X. dorsalis* where the presence of lignin (L), cellulose (C), and hemicelluloses (H), specifically xylan (X), was detected. Compounds were identified using Raman band assignments in Zeng et al. (2016) and Zhang et al. (2017). Spectra were acquired with a 532 nm laser at 10 mW with 30 s integration at 10× magnification and a 600 g/mm grating with a WITec alpha 300 R Raman system
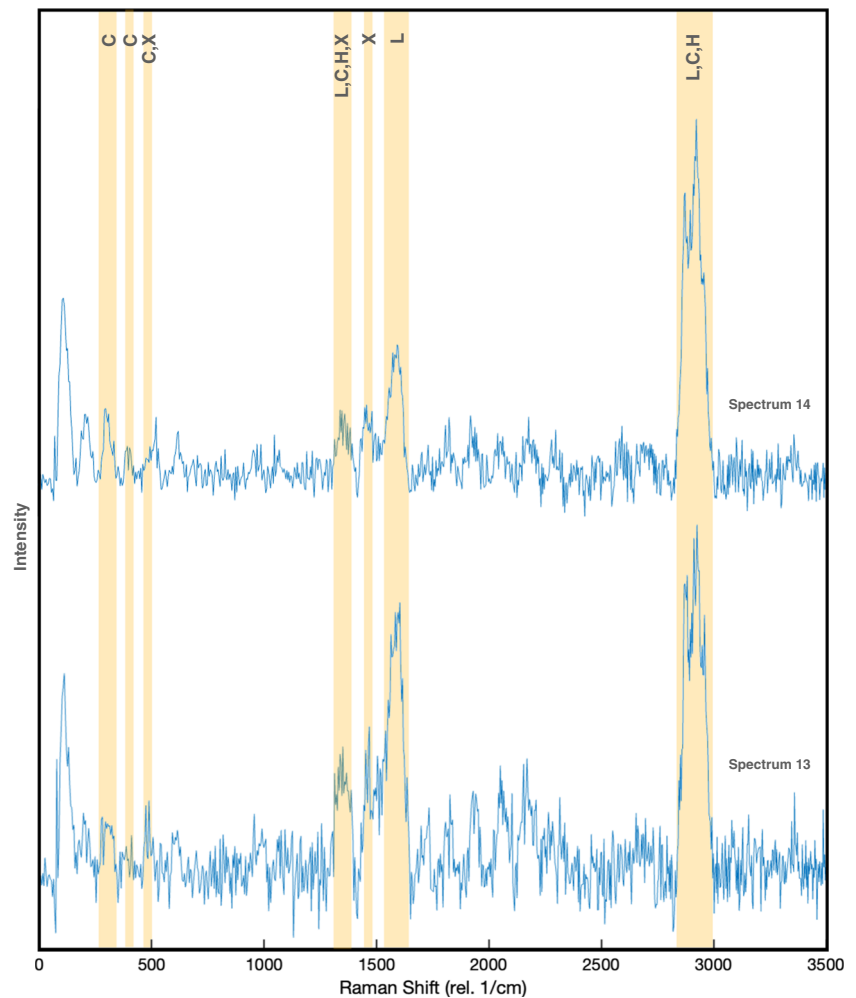
family limits our understanding of how and cannot support or refute the existence of a phylogenetic pattern.

The higher rates of recruitment, boring, and growth demonstrated in two species of the *X. dorsalis* clade (Romano et al. 2013; Amon et al. 2015a, 2015b) suggest that species of this clade act as exploitation competitors, consuming the limiting resource, wood, before competitors can do so. The fecal chimney may heighten their impact. This structure appears to us to impose two hydrodynamic disadvantages. First, the energy required for pumping the exhalant flow is apt to be increased because the chimney partially constricts the borehole and thus likely increases back pressure (Jørgensen and Riisgård 1988). Second, due to its poor separation from the inhalant flow, the excurrent flow risks refiltration of oxygen-depleted and dissolved CO_2-enriched water (Du Clos and Jiang 2018), unless the inhalant siphon is fully extended. In situ photos show this to be the case in this clade (Purchon 1941; Bernardino et al. 2010, Fig. 2B; Romano et al. 2014, Fig. 2). Siphonal extension had been thought to increase the animals' access to well-oxygenated seawater (Purchon 1941) or to facilitate opportunistic filter feeding (Voight et al. 2020); its role in minimizing refiltration (Monismith et al. 1990) had not been considered.

Given these liabilities, the fecal chimney must convey some benefit. Potentially it relates to the high concentrations of sulfide emitted by the sunken wood, at least early in deployments (Sandström et al. 2005; Yücel et al. 2013; Kalenitchenko et al. 2018). The siphons in the *X. dorsalis* clade lack calcium carbonate or periostracal protection as is common in other xylophagaids (Voight et al. 2019); they may risk sulfide poisoning (Goffredi 2017). Kalenitchenko et al. (2018) found sulfide concentrations to be lower in boreholes than in the surrounding wood, leading them to suggest that sulfide is oxidized in the borehole. However, our elemental analysis found no significant concentrations of electron receptors in the chimneys which would be predicted if this hypothesis were supported. Instead, we suggest the excurrent flow, by ventilating the borehole, rids it of sulfide, especially near the animal's vulnerable siphon. The fecal chimney's mucus lining may also minimize sulfide exposure and enhance bivalve survival by minimizing the inward diffusion of sulfide as do mucus linings in infaunal burrows (Aller 1983; Hannides et al. 2005; Zorn et al. 2006).

Composed primarily of lignin, the fecal chimney, perhaps with metabolites added by the bivalve's digestive system, could serve as a larval settlement cue and accelerate recruitment.

Larvae of xylophagaid's sister taxon, the Teredinidae, respond to chemical cues (Toth et al. 2015), including sawdust extract, malic acid, and other humic substances (Harington 1921). Fungi convert lignin to humic substances in terrestrial and freshwater systems (e.g., Khatami 2020). Although deep-sea fungi remain poorly known, they exist on sunken wood (Nagano et al. 2019). If fecal chimneys, perhaps chemically enhanced, cue xylophagaid larvae settlement, more chimneys and greater signal would result, up to a point. Because larvae explore the substrate before committing to metamorphose (Haderlie 1983), they may sense overcrowding and opt to avoid it.

As the population densities of members of the *X. dorsalis* clade increase in a given wood fall, the volume of fecal chimneys increases, and oxygen availability must decrease. As xylophagaids bore across the grain of the wood, the wood's vessel elements or tracheids may enhance the spread of hypoxia. Only animals tolerant of hypoxia, including species of the *X. dorsalis* clade, could survive in the habitat. The foot of *X. dorsalis* contains hemoglobin (Ansell and Nair 1968), and the larvae of *X. washingtona*, potentially the most sensitive phase of the life cycle, successfully recruit in oxygen concentrations of 0.42 mL/L (Muraoka 1965), considerably below that typical for marine invertebrates (Vaquer-Sunyer and Duarte 2008). Tolerance of hypoxia is unknown and untested in other xylophagaids, but none shows evidence of hemoglobin (JRV, pers. obs.).

Diversity in recovered wood deployments colonized by members of the *X. dorsalis* clade tends to be limited. Amon et al. (2015b) reported that of 7155 animals on a deployment bored by *X. indica*, 6850 were members of *X. indica*. Young et al. (2022) found five species formed 98% of the animals in a deployment bored by *X. oregona*; that xylophagaid species and the polychaete *Ophryotrocha langstrumpae* Wiklund et al., 2012, also known from whale falls (Wiklund et al. 2012), formed 80.9% of the species. Voight (2007) recovered a 10-month-old replicate deployment in which *X. oregona* composed 25% of the xylophagaids; 14 months later, 80% of the xylophagaids in the second replicate deployment were *X. oregona*. The limited biodiversity certainly reflects fewer predators, which likely increases xylophagaid survival. Why microsympatric xylophagaids were reduced is unknown, but oxygen limitation is recognized as a means of competition (Ferguson et al. 2013).

In exploitation competition, individuals interact indirectly as they compete for a limited resource. Among wood borers, the higher population densities and faster boring and growth rates known in the *X. dorsalis* clade are evidence that at least some of its members are adept exploitation competitors, using the finite and, to them, obligate resource wood faster than do other taxa. They lower oxygen availability to poison the habitat in the most base way, by retaining fecal pellets in their boreholes.

This study outlines evidence for exploitative competition in the deep sea. We hypothesize one xylophagaid clade evolved into a super competitor, recruiting, growing, and consuming the limiting resource more quickly than others can. Moreover, the fecal chimney, although appearing to be a liability to excurrent flow, may not only protect against the environmental toxin sulfide, but it may cue larval settlement. The resultant low-oxygen habitat may deter competitors intolerant of hypoxia. The significantly shallower average depth of species of the *Xylophaga dorsalis* clade (Voight 2008) places them where wood is predicted to be more abundant (Voight 2015), supporting the risky strategy used by these species. Largely immobile adults rapidly consume their habitat, and rapidly generate larvae that find and colonize other wood falls. Sympatric xylophagaids may seek refuge in other, stochastically distributed wood falls that are yet to be discovered by the *X. dorsalis* clade.

Declarations

Conflict of interest The authors declare no competing interests.

Ethics approval All applicable international, national, and/or institutional guidelines for animal testing, animal care, and use of animals were followed by the authors.

Sampling and field studies All necessary permits for sampling and observational field studies have been obtained by the authors from the competent authorities and are mentioned in the acknowledgements, if applicable. The study is compliant with CBD and Nagoya protocols.

Data availability Additional information from EDS and Raman Spectroscopy is available in the Online Resource.

Author Contribution MH and PGA conceived the question and designed the study. MH conducted fieldwork and labwork under PGA's supervision. MH and PGA analysed the data and wrote the manuscript.

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