

Evolutionary ecology of driftwood talitrids: a review

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<http://zoobank.org/ABA424BC-3256-4D13-9FDF-4D9C4FC46FC5>

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Abstract

Received 9 March 2017
Accepted 30 June 2017
Published 15 November 2017

Academic editor:
Matthias Glaubrecht

Key Words

Obligate xylophagous talitrids
dwarfism
interspecific squatting in gribble burrows
driftwood ecotope
facultative xylophagous talitrids

Marine driftwood, both when floating at the sea surface and after stranding in the supralittoral of a beach, has been inadequately sampled for talitrids throughout the world. It is probable that many more talitrids than the seven currently recognized as driftwood species are extant. Because they are obligate xylophages all seven species are considered to be specialized driftwood talitrids. They contrast with talitrids able to feed on either wrack or driftwood, as has been established experimentally in *Platorchestia platensis* (Krøyer, 1845). For the best known genus of specialized driftwood talitrids, *Macarorchestia*, there are two zoogeographic series: Northeast Atlantic: *M. microphtalma* – *M. roffensis* – *M. martini* and Mediterranean: *M. remyi* – *M. pavesiae*. Both geographic series are characterized by increasing dwarfism. Experimental studies suggest that dwarfism evolved to allow talitrids to occupy the small burrows made by gribbles (Isopoda, Limnoridae) in driftwood, and/or because driftwood was a poor quality food by comparison with wrack. The phylogenetic advantages of talitrids living in driftwood are that: they are protected from shorebird predation, they are provided with a long distance dispersal mechanism, and they have a relatively long term, albeit poorer quality, food source. Molecular genetic studies confirm that both *Macarorchestia* and *Neotenorchestia* have evolved by dwarfism from larger *Orchestia* ancestors.

Introduction

The Talitroidea are a superfamily of Gammaridean Amphipoda and among the families of which it is composed, the largest is the Talitridae (=talitrids) with over 250 species listed by Serejo & Lowry (2008). Talitrids are characterized by reduced uropod 3, with antenna 1 shorter than antenna 2, the mandible lacking a palp and with palp of the maxilla reduced (Bousfield 1973). Every year more species are added to the list, suggesting that the taxonomy is at an early stage of development. The current morphology-based taxonomy of the Talitridae is unsatisfactory (Lincoln 1979; Wildish 1988) for the following reasons:

- Perhaps 2 to 20 times less than the likely total species number within the family (~500–5000) have been collected and formally described
- Inadequate sampling effort is available to discover new species

- Too few taxonomists are available to formally describe the new species already discovered (e.g. Bousfield 1984)
- The powerful molecular genetic methods now available have not been applied adequately to further talitrid taxonomy
- Morphology-based phylogeny's are likely to suffer from convergence problems (see below)

Classification of talitrids at levels higher than the species is likely to suffer from convergence problems if it is based only on morphological criteria (Bousfield 1982). This caveat probably also applies to the morphology-based cladistics studies of Serejo (2004) and Lowry and Myers (2013). Modern molecular genetics has begun to be applied to the taxonomy of talitrids (e.g. Radulović 2012; Pavesi and Ketmaier 2013; Pavesi et al. 2013; Yang et al. 2013; Kim et al. 2013; Pavesi et al. 2014; Baldanzi et al. 2016; Wildish et al. 2016). Yet, a much wider

geographic coverage of talitrid species is required before phylogenetic patterns can aid in the higher classification of the Talitridae.

An alternative way of classifying talitrids is by the ecological habitats, or ecotopes, that they occupy. Talitrids are found on all continents, with the exception of Antarctica, in the following ecotopes: eulittoral or supralittoral wrack, supralittoral sandy beaches, supralittoral marshes, driftwood and caves which open in the supralittoral (Table 1). Besides these marine/estuarine habitats talitrids are found in freshwater and in true terrestrial habitats including semi-topical/ tropical forest plant litter, grassland and soil ecotopes. Talitridae are the only amphipod family to have representative species found in fully terrestrial habitats.

This is a review of the evolutionary ecology of those talitrids which are capable of living in both floating or stranded driftwood. We define the technical terms used in this presentation as follows:

Driftwood depository: that part of the marine supralittoral, often associated with salt marshes or small streams discharging to the sea, where significant amounts of driftwood accumulate (Wildish and Robinson 2016a).

Driftwood talitrids: an ecological grouping of talitrids specialized for obligately living in and feeding on rotting, damp driftwood as the primary ecotope (Wildish 1988).

Ecotype: a locally adapted population within a species which is characteristic of a particular ecotope (Lincoln et al. 1982).

Interspecific squatting: the relationship between two genetically different species, in which the builder inadvertently assists the occupier to find shelter. E.g. the use by a hermit crab of an un-occupied gastropod shell (Wildish and Robinson 2016a).

Primary ecotope: the particular habitat in which a species is commonly found and to which it has evolved characteristic adaptations (Wildish and Robinson 2016a).

Saproxylbios: those organisms living in, or on, rotting wood (Lincoln et al. 1982)

Secondary ecotope: the particular habitat in which a species is less commonly found and to which it lacks characteristic adaptations (Wildish and Robinson 2016a).

Wrack: dis-lodged marine macroalgae, either floating at the sea surface, or after stranding on a beach following tidal and wind action.

Xylophagous (= lignivorous, dendrophagous): said of an organism feeding on wood. (Lincoln et al. 1982)

Xylotomous. Used of an organism able to cut or bore directly into wood. (Lincoln et al. 1982)

Driftwood Specialist Talitrids

Presently known driftwood talitrids (Table 2) includes a total of seven species. As far as can be determined they are xylophagous (=lignivorous), obligately associated with driftwood and have not been found in other habitats. Part

Table 1. Classification of primary Talitrid ecotopes, with some examples of the ecotypes occupying them.

Ecosystem	Primary Ecotope	Ecotype examples
Marine/estuarine	Eulittoral wrack	<i>Orchestia mediterranea</i> <i>O. aestuarensis</i>
	Supralittoral wrack	<i>Orchestia gammarellus</i> <i>Mexorchestia</i> sp.
	Supralittoral sand burrowing	<i>Talitrus saltator</i> <i>Megalorchestia</i> sp.
	Supralittoral marsh	<i>Orchestia grillus</i> <i>Uhlorchestia uhleri</i>
	Supralittoral driftwood	<i>Macarorchestia remyi</i> <i>M. roffensis</i>
Freshwater	Supralittoral estuarine/freshwater wrack	<i>Cryptorchestia cavimana</i>
Terrestrial	Rainforest leaf litter	<i>Orchestia gomeri</i> <i>Palmorchestia epigaea</i>
	Cave living	<i>Palmorchestia hypogaea</i> <i>Minamitalitrus zoltani</i>
	Grassland	<i>Makawe hurleyi</i> <i>Puhuruhuru patersoni</i>
	Soil- burrowing	<i>Keratroides albidus</i>

Table 2. List of the known species of driftwood specialist talitrids recognized by 2017. N1 is the number of individuals reported as type material, N2 is the number of references which include each named species in the biological study reported. See Supplementary List for the full list of references.

Taxa	N1	N2	Zoogeographic area
<i>M. microphtalma</i> (Amanieu & Salvat, 1963)	20	8	North-East Atlantic
<i>M. roffensis</i> (Wildish, 1969)	418	24	
<i>M. martini</i> Stock, 1989	9	11	
<i>M. remyi</i> (Schellenberg, 1950)	7	29	Mediterranean Sea
<i>M. pavesiae</i> Wildish, 2014	15	2	
<i>Neotenorchestia kenwildishi</i> Wildish, 2014	10	2	NE Atlantic
" <i>Platorchestia</i> " <i>chatamensis</i> Bousfield, 1984	1	9	NW Pacific

of the reason for the paucity of species is that driftwood talitrids are rare and difficult to collect. Supralittoral stranded, driftwood must be seawater-dampened and at the right stage of microbial decomposition for the possibility that talitrids be present. Sampling requires cutting open the driftwood with a hand axe or chain saw. Only one species, *N. kenwildishi*, has been sampled from a floating, driftwood log which stranded on the rocky shore at the Lappel, Isle of Sheppey, U. K. (Wildish 2014). All of the other collections have been from already stranded driftwood which had been deposited in the high supralittoral, often in contiguous marshes. The rarity of driftwood specialist talitrids is emphasized by the small number of individuals included in the type series, N1, at the first description of each species (Table 2), or by the few references for each species (N2 in Table 2). A complete list of references for each driftwood talitrid is available as a Supplementary Reference List. For *P. chathamensis*, only a single adult female (Bousfield 1984), for *Neotenorchestia*: 9 juveniles and 1 immature male (Wildish 2014) and for *M. martini*: 1 adult male and 8 females (Stock 1989), were available as type specimens.

Driftwood talitrid taxonomy suffers from all of the problems mentioned in the Introduction, with the key one being an inadequate sampling effort. In fact only two geographic areas: the north-eastern Atlantic and Mediterranean coasts have been examined in a preliminary way for driftwood specialist talitrids. Further intensive geographic sampling within this area would be expected to yield more species. Intensive sampling of stranded driftwood in other parts of the world, particularly in southern temperate regions, is predicted to yield many more species.

Driftwood primary ecotype

A talitrid, *Macarorchestia roffensis*, from the Medway estuary, U.K., specialized for living permanently in driftwood was originally recognized by Wildish (1982), inclusive of the experimental demonstration that this species could live in culture solely on rotting driftwood for at least 6 months. A second talitrid population of *Macarorchestia remyi*, from the Tyrrhenian Sea, Italy was studied ecologically over a one year period and shown to be closely associated with rotting driftwood (Pavesi & De Matthaeis 2009). This lignivorous dependence by these two species of *Macarorchestia* probably extends to all five species listed in Table 2, because they have always been found associated with driftwood. We distinguish these ecotypes as primary because they show characteristic adaptations (see below) to the driftwood ecotope and to distinguish them from secondary ecotypes which facultatively utilize rotting driftwood and do not share characteristic driftwood adaptations. Wildish & Robinson (2016a) conducted a preliminary ecological study of driftwood depositories in Passamaquoddy Bay, Canada and in one of these at Hartley Cove found no driftwood specialist talitrids, but a generalist wrack talitrid which had acclimated to living in driftwood, as is discussed in the next section.

Driftwood secondary ecotype

The primary ecotype for *Platorchestia platensis* is as a wrack generalist (Bock 1967; Behbenhani and Croker 1982; Hodgson et al. 2014), but during an ecological study of a driftwood depository this species was found in rotting driftwood in significant numbers. Thus in a 45 x 10 x 10 cm piece of driftwood maintained in culture over 300 *P. platensis* were present and they were maintained solely on driftwood for > 6 months (Wildish and Robinson 2016a). *P. platensis* cultured in this way were found to have a significantly reduced basal metabolic rate in comparison with wrack-cultured *P. platensis* (Wildish and Robinson 2016b).

Driftwood ecotope

Woody wastes from both monocotyledonous and dicotyledonous plants have existed for over 120 MYA (Atlantic Geoscience Society 2001), that is to say for all of the geological time that talitrids split off from a hyalid-like ancestors some 110 MYA according to Bousfield (1984). The input of woody wastes on land occurs initially to freshwater as a result of leaf fall, branch fall as a result of lightning, to whole trees being eroded from river banks. The reception and fate of driftwood in freshwater ecosystems is relatively well studied (Stoklund et al. 2012). In addition to the natural input, in more recent times an anthropogenic input, inclusive of discarded lumber from wooden buildings, wharf pilings and ships has occurred. Some of the driftwood input reaches the marine ecosystem, via estuaries, or via direct input to the sea. Driftwood as a floating substrate for invertebrate hitchhikers has been reviewed by Thiel & Gutow (2005a) and Thiel & Haye (2006). However, the decay succession of marine driftwood is poorly known, but undergoes the general stages shown in Fig.1. After primary colonization by a specialized, halophytic microflora, consisting of fungi and bacteria, plus a few unique species of invertebrates such as gribbles (Isopoda, Limnoridae) and chelurid amphipods which are xylotomous, that is to say produce native wood degrading enzymes in their gut, and thus can burrow into fresh driftwood without the aid of microflora (Kern et al. 2013). Secondary colonizers follow, all of which are xylophagous, trophically relying on the wood degrading microflora in some as yet un-specified way. These include the driftwood specialist talitrids where studies on the physiology of digestion have been unable to demonstrate whether cellulases present in the talitrid gut originate from native sources, or from symbiotic gut microorganisms (Agrawal 1961; Wildish and Poole 1970; Johnston et al. 2005).

Other invertebrates which are xylophagous, secondary colonizers besides talitrids and which spend at least part of their lifecycle within decomposing driftwood include: termites, ants, isopods, centipedes, a variety of insect larvae, inclusive of beetles (Amanieu and Salvat 1963; Wildish 1982; Thiel and Gutow 2005b).

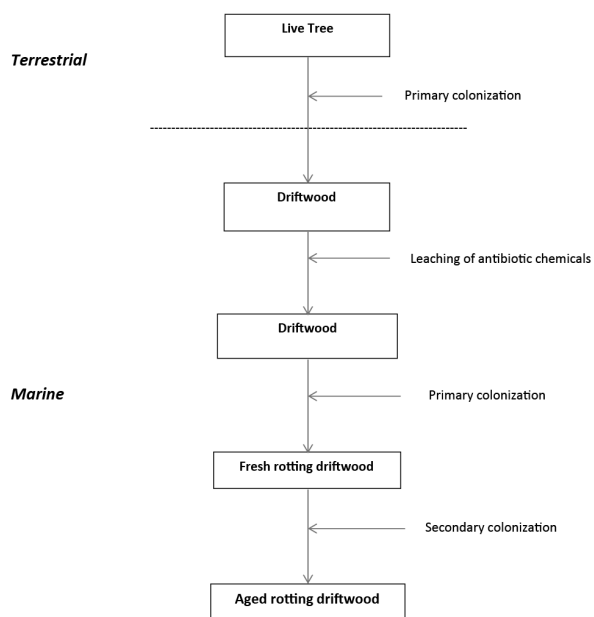


Figure 1. Driftwood decay succession in the marine/estuarine environment. Primary colonizers include cellulolytic fungi and bacteria, gribbles and chelurid amphipods. Secondary colonizers include talitrids, isopods, chilopods, insect larvae, ants, termites.

At some stage towards the end of the decay succession (Fig. 1) driftwood loses its buoyancy and if floating at sea, sinks. Some experimental studies in northern climates conducted to determine how long rafted timber can remain afloat, when it is floated down estuaries to the sawmill, have shown that it depends on the tree species and varies from 6 to 17 months (Hägglom 1982). It is probable that driftwood which sinks will result in the extirpation of any talitrid fauna. Commonly, natural driftwood will strand on a beach in the supralittoral and sometimes in a driftwood depository – a special location in the supralittoral where significant amounts of driftwood accumulate, often in salt marshes or where small streams empty to the sea (Wildish and Robinson 2016a). None of the driftwood contained primary ecotypical talitrids and only two of 50 marked driftwood specimens examined closely at the Hartley Cove driftwood depository contained secondary ecotype, *P. platensis* (Wildish and Robinson 2016a). Very few of the other driftwood specimens cursorily examined at Hartley Cove appeared to contain talitrids (usually because the driftwood was too dry) suggesting that *P. platensis*-occupation of driftwood was a comparatively rare phenomenon.

Zoogeography and dispersal of driftwood talitrids

Preliminary geographic sampling, using the special methods needed to sample stranded marine driftwood (see above) have only been completed in northeast Atlantic

and Mediterranean coastal regions. As far as is known, no concerted efforts have been employed to sample floating driftwood at sea. Because of the lack of geographic coverage in sampling driftwood it is probably premature to begin a discussion on the zoogeography of driftwood talitrids. However, for the genus *Macarorchestia*, some preliminary findings are available for the five, probably incompletely, known species (Wildish 2014). Thus there are two geographically separated species-groups of *Macarorchestia*, as follows:

- Northeast Atlantic: *microphthalma* – *roffensis* – *martini*, and
- Mediterranean: *remyi* – *pavesiae*

In both series there is a trend towards dwarfism (see total body length data for males and females in Pavesii et al. 2014).

Talitrid adaptations

Characteristic adaptations of driftwood specialist talitrids are contrasted with the other ecotypes shown in Table 3. Driftwood adaptations are closest to those for cave-living talitrids, with similarities which include small size, sexual dimorphism in which females are equal or larger than males, reduced pleopods and oostegites and the absence of dorsal pigment patterns. The two significant differences between the ecotypes are that eyes are small versus absent or vestigial and that the male second gnathopod is subchelate versus mitten-like, in cavernicolous talitrids.

Driftwood talitrids and their specialist adaptations

Most of the adaptations associated with currently known talitrids from a primary driftwood ecotope (Table 3) are morphological in nature. This is because so little is known about the physiology and behaviour of the driftwood specialist talitrids. Presented below is what is known about the driftwood talitrid specialist adaptations listed in Table 3.

The evolution of *Macarorchestia* and *Neotenorchestia* has involved dwarfism from a presumed larger wrack generalist ancestor. The underlying physiological changes involved in dwarfism are reduced growth rates in *M. roffensis* (Wildish 1982) and reduced basal metabolic rates in *M. remyi* (Wildish et al. In preparation). In addition the onset of sexual maturity begins at an earlier moult stage in *M. roffensis* (Wildish 1982). This means that slower growing driftwood specialist talitrids have fewer moults per life history than wrack generalist ones, such as *Orchestia*.

The reduction in body length within *Macarorchestia* varies between the sexes (data in Table 4, Pavesi et al. 2014). In the largest, *M. microphthalma*, body length is

Table 3. Characteristic adaptations of talitrids (mainly from the Northeast Atlantic and Mediterranean Sea regions).

Morphological characteristic	Wrack generalist	Sand burrowing specialist	Driftwood specialist	Cave-living specialist	Rainforest leaf litter generalist
Body length(TBL), mm	>15	>15	<15	<15	<15, >15
TBL, sexual dimorphism	M>F	M>F	F>M	F>M	F>M, M>F
Male gnathopod 2 subchelation	Strongly subchelate	Mitten-like	Subchelate	Mitten-like	Subchelate or mitten-like
Peraeopod length of 6 and 7	Long	Medium	Short	Very long	Short/long
Eye size	Medium	Large	Small	Vestigial/absent	Small/medium
Pleopod size	Large	Large	Medium/small	Small	Small/large
Oostegite size	Large	Large	Medium/small	Small	Small/large
Dorsal pigment patterns	Present	Present, or reduced	Absent	Absent	Present/absent

Table 4. Maximum total body length, mm (TBL) of adult female *Macarorchestia* from Pavesi et al. (2014), equivalent body depth, mm (BD) predicted from equation shown in the text and estimated percentage of available gribble burrows each taxon can occupy, based on data from the Bay of Fundy (Wildish and Robinson 2016a).

Taxa	TBL, mm	BD, mm	% of gribble burrows each taxon can occupy
<i>M. microphtalma</i> (Amanieu & Salvat, 1963)	13.94	1.92	58.2
<i>M. renyi</i> (Schellenberg, 1950)	11.47	1.60	76.1
<i>M. pavesiae</i> Wildish, 2014	9.36	1.33	87.1
<i>M. roffensis</i> (Wildish, 1969)	8.30	1.19	91.9
<i>M. martini</i> Stock, 1989	6.22	0.92	98.0

only slightly larger in the male, whilst in the series of successively smaller species down to the smallest, *M. martini*, adult females are larger than males. This suggests less competition by smaller male driftwood talitrids for mates, because among larger wrack generalist the males out-compete smaller ones during mating (Williamson 1951). An opposing evolutionary imperative is that smaller body size forces a reduced reproductive output (Wildish 1979), which is counter-measured by female size being reduced as little as possible. Male second gnathopod subchelae are used in clasping females for copulation as in *Orchestia* (Wildish 1979), but their relatively small size implies that they are less useful in agonistic threats during male competition for mates.

Driftwood specialist talitrids spend much of their life in small confined spaces: typically in empty gribble (Isopoda, Linnoridae) burrows. The diameter of these burrows in driftwood ranges from 0.6 to 5 mm in diameter (Wildish and Robinson 2016a) in the Bay of Fundy. Presuming that similar gribble burrow diameters apply on the northeast Atlantic coasts of Europe leads to the assumption that peraeopod lengths are reduced in *Macarorchestia*, so they can better negotiate the narrow burrows they occupy.

A further result of spending much of their life cryptozoaically within driftwood is the lack of need for vision for foraging, astronomical-mediated locomotion and predator avoidance (Scapini 2006). Senses such as tactility and chemosensing become more important in the cryptozoic environment within driftwood. Consequent reduction in size and importance of eyes is to be expected. However, a complete loss of eyes, as occurs in some cave living specialist talitrids (Bousfield and Howarth 1976), does not occur in driftwood specialists. This may be because driftwood talitrids need to move to a new driftwood habitat,

where eyesight to locate it and to avoid bird predation is still an advantage.

Both pleopods and oostegites are reduced relative to body length (compared to *Orchestia*). Pleopods are functional in swimming and when stationary in seawater of drawing a current across the ventral body groove, for respiratory exchanges. Because of dwarfism and lower basal metabolic rate the ventilator current need not be as energetic as in larger, more active wrack generalist talitrids. Consequently the evolutionary process supports a reduction in pleopod size. For oostegites the small body size of driftwood talitrids dictates a smaller reproductive output, as fewer ova per brood (Wildish 1979). Brood numbers for three species of *Macarorchestia* are shown in Wildish et al. (2012) and demonstrate the effect of decreasing body size dictating fewer ova/brood. This obviates the need for large, extensive oostegites which are a requirement when many ova are in the brood pouch.

The function of dorsal pigment patterns in wrack generalist talitrids has been hypothesized to be as camouflage from shorebird predators (Wildish and Martell 2012; Wildish and LeCroy 2013). As driftwood specialist talitrids are rarely away from their driftwood burrows their need for camouflage is minimal. Consequently, the deposition of pigments in the integument of driftwood species is dispensed with.

Ultimate causes of dwarfism in driftwood specialist talitrids

Three hypotheses were experimentally investigated as environmental triggers for dwarfism in driftwood specialist talitrids (Wildish and Robinson 2016b):

- Small size reduced the absolute quantity of dissolved oxygen needed during dispersal at sea. The environmental trigger was low availability of dissolved oxygen within driftwood.
- That driftwood was a poor diet and forced slower growth
- That smaller size allowed driftwood living talitrids to occupy many more of the available empty gribble burrows, which are commonly present in driftwood.

The first hypothesis was discarded because model calculations showed that all talitrid sizes would be limited by oxygen availability in static conditions. In fact such conditions would not occur within gribble burrows because talitrid pleopod beating would induce a ventilatory current across the ventral respiratory surfaces, thus preventing oxygen starvation.

Both of the next two hypotheses were supported by physiological and behavioural experiments. Culture experiments in which a driftwood specialist, *M. remyi*, and a wrack generalist, *P. platensis*, were fed driftwood, resulted in a reduced basal metabolic rate and consequent reduction in growth rate in comparison with wrack fed *P. platensis*. Recent experiments (Wildish et al, In preparation) have shown that the driftwood-fed *P. platensis* acclimates, rather than adapts to the driftwood ecotope. Such experiments suggest how driftwood talitrids could evolve from wrack generalists by initial acclimation to feeding on driftwood by lowering basal metabolism and growth. Presumably this would eventually be genetically fixed in driftwood specialist ancestors.

The above results do not explain how serial dwarfism observed in *Macarorchestia* species could occur. Perhaps the behavioural experiments, designed to examine the last hypothesis listed above can do so. In these experiments it was shown that talitrids were limited by body size to the gribble hole diameter that they could negotiate. The measurement of body depth (BD) proved to be the best indicator of body size which could negotiate a particular diameter of gribble burrow, in behavioural experiments on this point (Wildish and Robinson 2016b). Consequently the regression equation for BD on total body length (TBL) for a population of *M. remyi* from Principina-a-Mare, Italy, was used as follows:

$(BD) = 0.1298(TBL) + 0.1115$, $N = 24$, $R^2 = 0.89$. TBL size range from 7.0 to 20.5 mm.

If we assume that the same relationship applies to all species within *Macarorchestia*, we can predict from this equation what burrow diameter each species can occupy. The results are shown in Table 4 and by comparison with the observed frequency of gribble burrow diameters, the percentage of gribble burrows each species can occupy can be calculated. Thus the smallest species, *M. martini*, can negotiate nearly all of the smallest gribble burrows, whilst the largest, *M. microphtalma*, is limited to only 58% of the available burrows.

Land colonization and the contiguous habitat hypothesis

In an earlier review which included land colonization by talitrids (Wildish 1988) the evolutionary process was based on the juxtaposition of ecotopes and the likely possibility that passive or active migration would carry talitrids into an adjacent ecotope. One example of this contiguous habitat hypothesis is provided by the genus *Palmorchestia* endemic on the Canary Islands (Stock and Martin 1988; Stock 1990). It was proposed that ancestors of the genus arrived on La Palma, Canary Islands as a driftwood talitrid, was passively carried into a cave by tidal action, where it evolved into the cavernicolous talitrid: *Palmorchestia hypogaea* (Wildish 2012). By dispersal within the natural lava tubes which permeate La Palma ancestors of this species emerged into the contiguous, subtropical rainforest, where they evolved into the terrestrial talitrid, *Palmorchestia epigaea*. Molecular genetic studies by Villacorta et al. (2008) support this view, including the finding that both species were closely related and that the cave-living *Palmorchestia* was older than the rainforest leaf-litter form. Villacorta et al. (2008) also presents genetic evidence that two Canary Island endemic terrestrial talitrids: *Orchestia guanacha* and *O. gomeri* are close phylogenetically to the wrack generalist *O. gammarellus*. This finding supports the contiguous habitat hypothesis that ancestors of a wrack generalist talitrid crossed, either actively or passively by tidal/wind action, the terrestrial boundary and adapted to rainforest leaf litter. A possible scenario for talitrid land colonization is depicted in Fig. 2, with evolutionary pathways having some molecular genetic support shown by solid arrows. Bousfield (1984) proposed that in the Lower Cretaceous (110-135 MYA) ancestral hyalids gave rise to freshwater hyalellids, intertidal hyalids and ancestral talitrids. Then in the Middle Cretaceous (90-110 MYA) the main talitroid lines diverged. One of these was the non-cusped terrestrial talitrids originating at ~105 MYA. The *Palmorchestia* evidence presented above suggests that land colonization may have recurred repeatedly throughout talitrid evolution and thus the phylogenetic picture for this group may be replete with convergencies.

The finding by Wildish and Robinson (2016a) that the wrack generalist, *Platorchestia platensis*, can occur occasionally in driftwood as a secondary ecotope provides further support for the contiguous habitat hypothesis. Additional evidence is that on the northeast Atlantic coast the wrack generalist, *Orchestia gammarellus*, is also occasionally found in marshes (Dias and Sprung 2001; Schrama et al. 2015). It seems general that talitrids well adapted to one type of ecotope, will occasionally be found in an adjacent one, as long as the environmental conditions (biotic and physical including humidity, temperature, decaying plant material, etc) permit it.

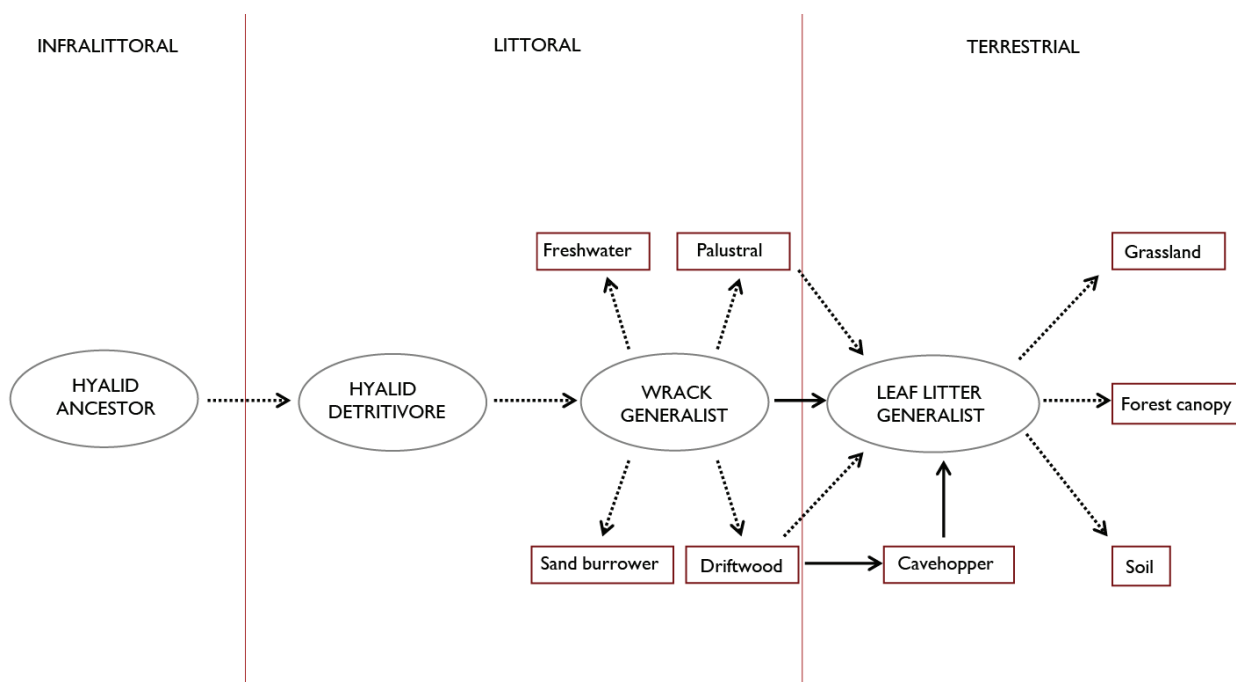


Figure 2. Hypothetical pathway of land colonization by talitrids. Oval boxes are generalists, oblong boxes are specialists. Dashed arrows are hypothetical and those with solid arrows indicate some genetic evidence.

Talitrid transfer between driftwood specimens

Because each driftwood specimen in which talitrids are residing has a finite life during the decay process, we know that there must be exchange from one driftwood specimen to another. When, and at what talitrid life history stage this re-colonization occurs remains a mystery. The transfer may be different depending on whether the talitrid involved is occupying a primary or secondary ecotope.

For primary, driftwood, ecotypical talitrids who appear to spend all their life history within damp, rotting driftwood, the most plausible location for exchange between driftwood specimens would be within a driftwood depository. Here driftwood specimens at all stages of the decay cycle are present and may be closely aligned to each other. As the old driftwood disintegrates nearby driftwood specimens are available to accept emigrating driftwood talitrids. However, no field observations are available which have observed driftwood transfer. Clearly further field and laboratory behavioural observations are needed to answer this question. This would include measuring the periodicity of locomotory activity in a representative driftwood specialist talitrid, as is already available for wrack generalists (Wildish 1970).

In secondary ecotypical talitrids the nature of the driftwood transfer is subtly different. Here the adoption of driftwood as a shelter and source of food occurs as part of the contiguous habitat hypothesis. Thus if wrack is scarce or unavailable wrack generalist talitrids, such as *P. platensis*, are able to acclimate to driftwood, but can

return to feeding on wrack if it becomes available again (Wildish & Robinson, In preparation).

Discussion

It is obvious from this review that all aspects of the biology of driftwood talitrids – either those occupying it as a primary or secondary ecotope – are at a very early stage of development. Thus all aspects of the biology of driftwood talitrids are in need of further work. To emphasize research projects of most use in advancing an understanding of the study of the evolutionary ecology of driftwood talitrids the following are listed:

- World-wide search for talitrids in driftwood, particularly where driftwood depositories are present
- More research on molecular genetic methods as it is applied to talitrid phylogeny and taxonomy
- Develop experimental methods that can be used to distinguish primary from secondary ecotypes
- Ecological studies on the decay succession of driftwood: inclusive of mass balances of driftwood to the oceans; microbial organisms, pathways and products involved in wood decay; secondary driftwood colonizers and how talitrids interact ecologically with the other invertebrates present in driftwood
- Physiological studies of digestion to resolve the role of microbes and how they are utilized in the talitrid gut
- Molecular genetic studies of driftwood talitrids and their potential ancestors, to provide a phylogeny of the driftwood talitrid ecological group

- Identification of the genetic and hormonal system which initiates sexual development in talitrids
- Experimental testing of the assumptions made in constructing the gribble burrow squatting hypothesis
- Behavioural studies with driftwood talitrids in primary and secondary ecotopes.

Some of the above are suitable as post graduate research projects and their completion will establish the evolutionary ecological study of driftwood talitrids on a much firmer scientific foundation.

Acknowledgments

Thanks to Dr. Laura Pavesi and an un-named reviewer for improving an earlier version of this manuscript.

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Supplementary material 1

List of References to Driftwood Talitrid species compiled by David Sheppard, Fisheries and Oceans Library, Bedford Institute of Oceanography

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Band/Volume: [93](#)

Autor(en)/Author(s): Wildish David J.

Artikel/Article: [Evolutionary ecology of driftwood talitrids: a review 353-361](#)