Species and functional trait turnover in response to broad-scale change and an invasive species

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Abstract. While beta diversity has been implicated as a key factor in controlling resilience of communities to stressors, lack of long-term data sets has limited the study of temporal dynamics of beta diversity. With a time series at two sites in excess of 40 yr, we investigated turnover of both species and functional traits in a system stressed by eutrophication and overfishing and undergoing climate change and invasion. The two sites, although located near to each other, differ in water depth (20 *cf.* 35 m), but both sites have displayed increased abundances of an invasive polychaete since 1990. We tested two hypotheses related to the effect of an invasive species; that taxa richness and turnover would decrease, and trait richness would increase post invasion and that trait turnover would increase between arrival and establishment of the invasive. Generally, we observed different dynamics at the two sites and responses not consistent with our hypotheses. We detected an increase in taxa richness at both sites and an increase in taxa turnover and number of traits at one site only. Trait turnover was higher prior to the invasion, although again only at one site. Disjunctive responses between species and trait turnover occurred, with the invader contributing in a nonrandom fashion to trait turnover. The lack of strong, consistent responses to the arrival and establishment of the invasive, and the decrease in trait turnover, suggests that effects of invasives are not only system- and species-dependent, but also depend on community dynamics of the invaded site, in particular the assembly processes, and historical context.

Key words: anthropogenic stressors; beta diversity; climate change; temporal dynamics; time series.

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INTRODUCTION

Biodiversity remains an enduring area of study for ecologists. Increasingly, studies are turning from descriptions of biodiversity to studying the effect of, and reasons for, changes in alpha, beta, and gamma biodiversity. In light of increasing global pressures such as climate change, hypoxia, eutrophication, and invasive species, beta diversity has been implicated as a key factor in defining resilience (Hughes et al. 2007, de Juan et al. 2013, Tanentzap et al. 2013, Buendia et al. 2014). At the same time, the use of biological traits to investigate functional stability, diversity, and redundancy is being highlighted (Statzner et al. 2004, Mouillot et al. 2006, 2013, Mason and de Bello 2013), suggesting that studies on temporal patterns in functional trait diversity, both natural and in response to changing environmental conditions, may prove fruitful.

Most studies of relationships between richness and turnover focus on spatial relationships

and, inevitably due to the relative newness of trait literature, on species richness and turnover. Temporal changes in species richness are well studied in the disturbance-recovery and invasive species literature, where invasion is predicted to reduce and homogenize species richness (i.e., reduce both species richness and turnover; Gordon 1998, Clavero et al. 2009). This reduction in species richness may vary with length of time since invasion (Strayer et al. 2006, Clark et al. 2013) and the background diversity of the system invaded (Villnäs and Norkko 2011). Following these generalities, species turnover would also be expected to vary with invasion, increasing as native species extinction at, or dispersal from, the invaded site increases, although, this prediction requires time-series data prior to invasion for validation.

There have been a number of studies comparing species and trait diversity, although these mainly compare richness (but see Fukami et al. 2005), and again focus on spatial aspects. No consistent relationships have been observed; indeed differences between species and trait diversity are reported to reflect differing community assemblage processes (Pavoine and Bonsall 2011, Spasojevic and Suding 2012). Disjunctive responses of species and trait diversity to change are expected to be more likely where communities within similar environments are driven by niche-based assembly processes (e.g., Swenson et al. 2011, Siefert et al. 2013), or where initial community composition (historical context) is important (Fukami et al. 2005). This makes it difficult to predict the generalities of trait diversity responses to change from studies on taxonomic responses.

Temporally, functional trait composition of forest communities changes faster than expected after acute disturbances (Swenson et al. 2012), thus increasing functional turnover. Successful invasive species are often expected to be functionally distinct (Vitousek 1996, Parker et al. 1999, Fargione et al. 2003), but the effect that the addition of a single species (albeit an abundant one) would have on the functional turnover in time is difficult to predict. If niche-based assembly processes are driving functional turnover, the effects of addition of a new, functionally distinct species may be minimal.

The Baltic Sea offers an ideal opportunity to investigate temporal patterns in species and functional diversity. Regular monitoring has been conducted at a number of stations since the 1960s and there is a large degree of knowledge about the species inhabiting it. It is a young ecosystem encompassing a limited number of benthic species (Bonsdorff 2006). The sea has a long history of disturbance in the form of eutrophication and accompanying hypoxia (Österblom et al. 2007, Carstensen et al. 2014). The low diversity and frequently occurring disturbances create possible vacant niches for invasive species. Indeed, the major part of the seafloor communities of the Baltic Sea has been invaded by an infaunal polychaete complex, *Marenzelleria* spp., since the middle of the 1980s (Leppäkoski and Olenin 2000). In the 1990s, this polychaete complex reached the Finnish coast (Norkko et al. 1993, Stigzelius et al. 1997), and gradually became a permanent, highly abundant member of the benthic communities (Kauppi et al. 2015). As the adult individuals of *Marenzelleria* tolerate stressful hypoxic conditions and generally live deeper in the sediments than the native species, it is potentially filling a vacant niche in the system (Leppäkoski and Olenin 2000, Norkko et al. 2012).

We use macrofaunal data collected from two coastal stations in the Gulf of Finland (Northern Baltic Proper) to investigate temporal patterns in species and trait richness and turnover. In particular, we examine changes relative to the arrival and establishment of an invasive. We test two hypotheses: (1) whether an invasive species in a system with a variable environment reduces species richness and turnover; and (2) whether functional trait richness and turnover increase with arrival, but decrease again once the invasive is established, when the invasive fills a vacant niche. We also examine (3) whether the inclusion of *Marenzelleria* traits into the system result in nonrandom trait turnover during arrival and after establishment.

Methods

Long-term annual data, collected in autumn, was available from two sites near Tvärminne Zoological Station, at the entrance to the Gulf of Finland, in the northern Baltic Sea. The two sites are close to each other (approximately 1 km apart); one at 20 m (shallow) and the other at 35 m (deep). Both were sampled in

1926 and 1928 and then approximately annually from 1964 to 2011 (missing years at deep site; 1965, 1980–1983, 1986–1987, and shallow site; 1975, 1980, 1982, 1986–1987). Data consisted of the average (of five replicates) abundance of macrofauna from a Van Veen Grab Sampler (1115 cm^2), sieved on 1.0-mm sieves, generally identified to species level (with the exception of Chironomidae and Oligochaeta).

Data between 1964–2007 has been described by Rousi et al. (2013) who attributed changes in macrofaunal composition to a mix of multiyear cycles in surface temperature and salinity, a small long-term decreasing trend in oxygen saturation (<1 mg/L over 30 yr) and variations in total phosphorus. Compositional changes included changes in the abundance of three dominants: decreases in the abundance of the amphipod *Monoporeia affinis* over the 1980s, and increases in the bivalve *Macoma balthica* (from the mid-1980s) and *Marenzelleria* spp. (during the 1990s). *Monoporeia affinis* is a small amphipod, with a moderate generation time (2–3 yr) without a larval dispersal stage. *Macoma* is a large, deposit-suspension feeding bivalve which can live up to 10 yr, with large individuals playing a major role in nutrient cycling (Norkko et al. 2013). *Marenzelleria* lives for 2–3 yr, is moderate in size and its larvae disperse in the water column. It has demonstrated effects on sediment bioturbation depth (Quintana et al. 2011, Renz and Forster 2013), organic matter burial (Josefson et al. 2012), and nutrient recycling (Hietanen et al. 2007, Norkko et al. 2012).

Functional trait determination

A set of biological trait information was available from earlier published classifications and taxonomic and morphologic sources of information (Villnäs et al. 2012, 2013). Categories used were those likely to affect ecosystem functions and resilience, either separately or in combination: feeding method (surface deposit feeder, burrowing deposit feeder, suspension feeder, carnivore, herbivore); sediment mixing or stabilization (tube mat, bio- and gallery diffusers); adult size (<0.001, 0.001–0.01, 0.01–0.1, 0.1–1.0 g), longevity (<1, 2–3, 3–5, 5–10 yr); mobility (stationary, swimming, crawling), reproductive mechanism (larval, brooding); and living position (pelagic, epibenthic, 0–2 cm sediment, >2 cm sediment).

Analyses

For the 1926–2011 time period, changes in multivariate community and trait composition were visually assessed to provide basic information on temporal patterns using nonmetric multidimensional scaling (nMDS) of Bray–Curtis similarities based on raw data. Correspondence analysis and similarity percentage analysis were used to explore which species and traits were driving the differences. As the two methods produced similar results, in the text we use species contributing >10% to the dissimilarity between periods as calculated by SIMPER (Primer E, Clarke and Gorley 2006).

Taxa turnover was calculated as $(\gamma/\alpha - 1)$ (Whittaker 1960) on presence/absence of data between pairs of subsequent years (where γ is the total number of taxa found in both years and α is the average taxa richness). Functional trait turnover between pairs of years was calculated based on presence/absence of biological traits (Bremner 2008, Hewitt et al. 2008). Use of pairs of subsequent years for calculating turnover ruled out the use of the 1926/28 data; however, an indicative turnover based on the difference between the 2 yr gap is given in the figures.

Hypotheses 1 and 2 required testing differences, at each site, for the number of taxa and taxon turnover and the number of traits and trait turnover respectively, between three periods: before *Marenzelleria* spp. arrived (1964–1990); arrival of *Marenzelleria* until density was consistently >5% of the total (1991–2004); and established (2005–2011). Time series within each period were checked for autocorrelation using the Durban–Watson statistic before using the nonparametric Kruskal–Wallis test (with ties). However, as ties occurred and the sample sizes in at least one period were >5, the chi-square approximation to the Kruskal–Wallis with 2 degrees of freedom (number of groups minus 1) was used.

Actual traits that exhibited turnover were identified and presented as a percentage of the time series. Abundance of specific traits was calculated for four of the functional categories: adult size, longevity, feeding type, and sediment mixing categories, and a Friedman's test (approximated by the Cochran–Mantel–Haenszel statistic) was used on each category to determine whether abundance of traits changed ranking in the different periods.

Whether the presence of *Marenzelleria* resulted in nonrandom turnover of traits (question 3) was determined by 100 Monte Carlo simulations. The presence of *Marenzelleria* was allotted randomly (with replacement) to the trait matrix and the resultant frequency of traits that exhibited turnover were calculated and compared with the observed frequencies in the arrival and establishment periods at each site separately.

Results

The community composition at the two sites was not strongly different (average dissimilarity of 66%). Differences were driven by higher abundances of *Monoporeia affinis*, *Pontoporeia femorata* and *Marenzelleria* spp. at the deep site and higher abundances of *Macoma balthica* at the shallow site. However, the temporal patterns in community composition differed between the 2 sites (Fig. 1). At the deep site, the community composition observed in the 1920s was distinctly different to that observed at any other time, (reflecting highest abundances of *M. affinis*). At the shallower site, community composition in the 1920s was similar to that post 1991, reflecting similar abundances of *M. balthica*. Community composition at the shallower site was also more variable between 1964 and 1990 than at the deep site.

The two sites differed less functionally, with an average dissimilarity of 53%. Dissimilarity reflected higher abundances of individuals living 2–3 yr, or being brooders, biodiffusers, swimmers, or small at the deep site. The overall temporal patterns were similar to those in community composition (Fig. 1).

At both sites, community and trait composition changed dramatically in the early 1990s. At the deep site, the before and arrival periods were 82% dissimilar in terms of community composition, driven by higher abundances of *Monoporeia affinis* and lower abundances of *Macoma balthica* in the before period. This same pattern was observed at the shallow site where the two periods were 81% dissimilar. Trait composition of the two periods at the deep site were 71% dissimilar, reflecting higher abundances of brooders, medium life span (2–3 yr), and biodiffusers in the before period. The same traits contributed in the same way to dissimilarities between the two periods at the shallow site, although the two periods were only 65% dissimilar.

Dissimilarities of 62% and 40% in community composition between the arrival and the established period were observed at the deep and shallow sites, respectively. In both cases, this reflected higher abundances of *Marenzelleria* spp. in the established period, but at the deep site *Macoma balthica* also had higher abundances, while at the shallow site *M. balthica* had lower abundances in the established period. Reflecting changes in community composition, trait composition also changed between the arrival and the established period, and again dissimilarities between the two periods were greater at the deep site (49%) than at the shallow site (26%). At the deep site, dissimilarities were driven by higher abundances in the established period in the larval dispersal, gallery diffuser, medium life span and medium size traits, all traits associated with *Marenzelleria* spp., although *M. balthica* also has a larval dispersal stage. At the shallow site, no traits contributed >10% to the dissimilarity, but higher abundances during the established period were observed for the larval dispersal trait and lower abundances of the biodiffuser trait (*M. balthica*).

Hypothesis 1

A significant difference in taxa richness between the three periods was found at both sites (KW = 16.27, P = 0.003, shallow site; KW = 7.25, P = 0.0267, deep site), with number of taxa unexpectedly always greater in the establishment period and least in the before period (Fig. 2a). This was accompanied by a significant increase in taxa turnover at the shallow site only (KW = 9.48, P = 0.0087, shallow site; KW = 3.35, P = 0.1872, deep site). For both sites, variability in taxa turnover ranged between 0 and 0.56, with a marked increase starting in 1989, just before the invasion (Fig. 2b). Prior to 1980, values were much lower (0–0.34 at the shallow site and 0–0.29 at the deeper site), while post this period they varied between 0.1–0.56 with an average of 0.29.

Hypothesis 2

Variation between the three periods in the number of functional traits and functional trait turnover was not consistent between the two sites (Fig. 2c & d). No significant differences
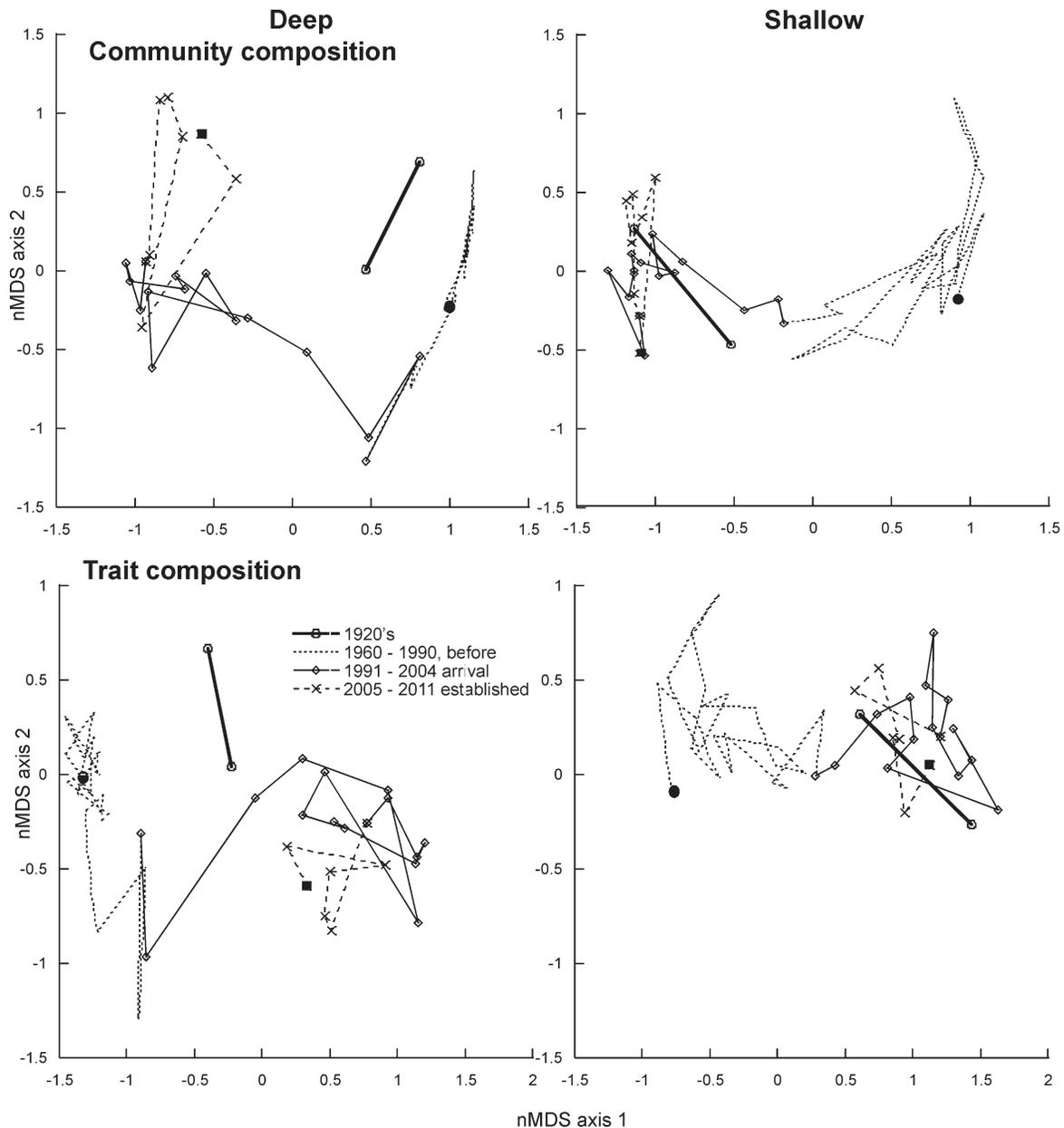
Fig. 1. Nonmetric multidimensional scaling ordination plot of changes in community and trait composition over time at the two sites, shown in two dimensions (stress level 0.06 and 0.05 for community and traits, respectively). Black circle = 1964, black square = 2011. Thicker line joins the two 1920s years. Years missing are 1965, 1980–1983, 1986–1987 at the deep site and 1975, 1980, 1982, 1986–1987 at the shallow site. Note that the two sites were analyzed together so that their relative differences can be examined by directly comparing the site plots.

were observed at the shallow site (KW = 4.10, P = 0.1286, number of traits; KW = 2.15, P = 0.3399, trait turnover). However, at the deep site number of traits was lowest in the before period (KW = 8.83, P = 0.0121), but trait turnover decreased when *Marenzelleria* spp. arrived, with trait turnover highest in the before period (KW = 6.31, P = 0.0425).
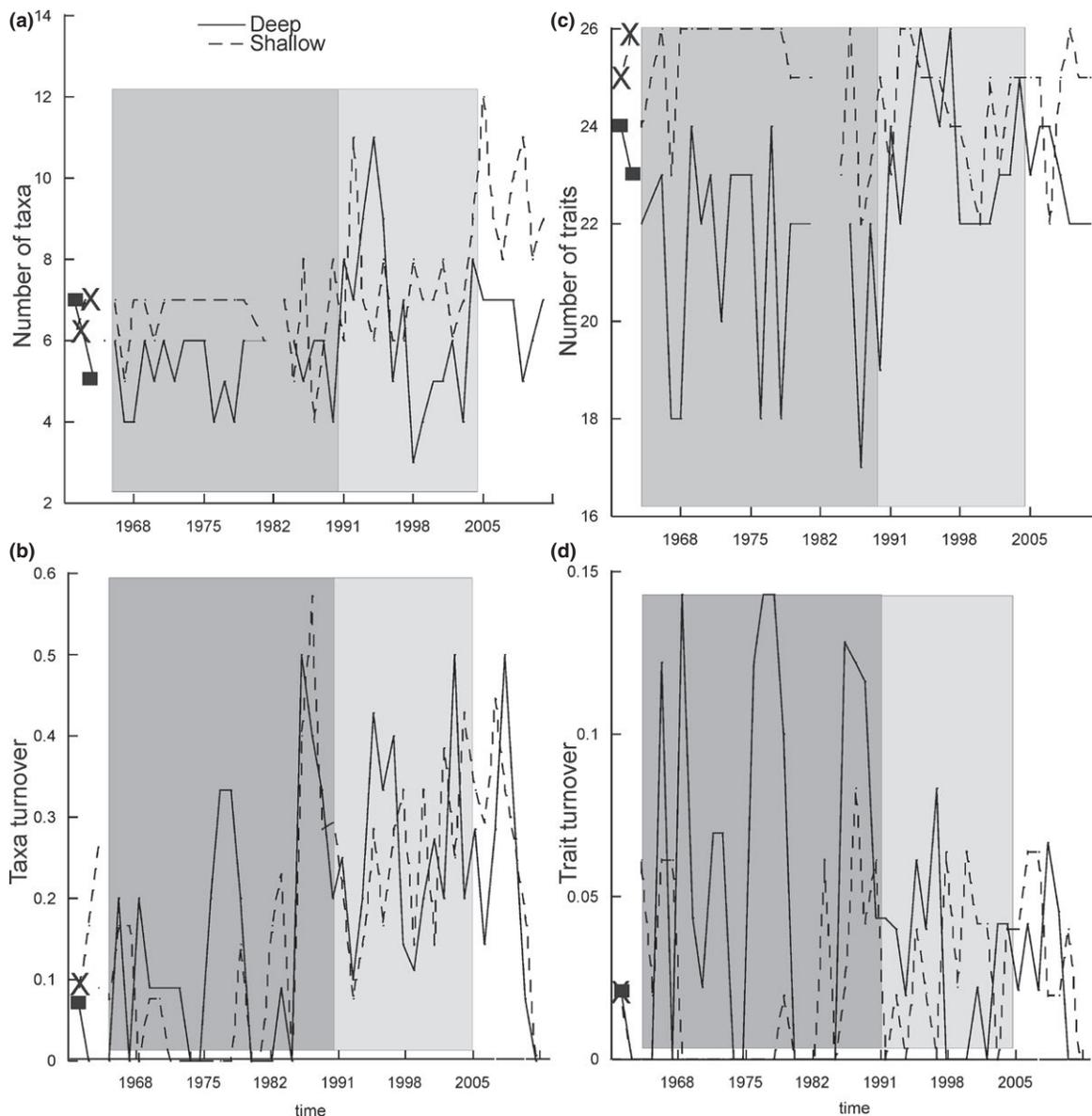
Fig. 2. Temporal patterns in taxa and trait richness and turnover at the two sites. The solid square and cross are data at the deep and shallow sites, respectively between 1926 and 1928. *Marenzelleria* spp. invaded the sites in 1991 and by 2005 was considered to be established. Dark and light gray shading designate the before and arrival time periods. See Fig. 1 caption for missing years.

Specific traits exhibiting turnover

The highest number of functional traits contributing to turnover occurred at the deep site in the before-time period (Table 1). Aside from this, six functional traits were turning over at both sites during the arrival time, and four over the established-time period. Although the same number of traits were involved at both sites, in both time periods only 50% of the traits were the same between the two sites. Interestingly, at both sites, 50% of the traits were the same between the arrival and established periods. Only one trait (living for <1 yr) contributed to turnover at both sites in all time periods.

Variance over time in the relative dominance of age traits was associated with the invasion of

Table 1. Proportion of times a trait contributed to turnover in the three time periods.

Traits	Deep site			Shallow site		
	Before	Arrival	Established	Before	Arrival	Established
Suspension feeder	0.56	0	0	0	0	0
Burrowing detritivore	0	0	0	0	0.14	0
Herbivore	0.61	0.14	0	0	0	0
Stationary	0.39	0	0	0	0	0
xs (<0.001 g)	0.11	0.43	0	0.33	0.21	0.50
<1 yr	0.17	0.21	0.33	0.22	0.14	0.67
1–2 yr	0.11	0.43	0.33	0.33	0.07	0
3–5 yr	0.06	0	0.33	0.33	0.71	0.50
Larval	0.17	0	0	0	0	0
Tube dweller	0.39	0.14	0.50	0	0	0
Gallery diffuser	0.61	0.14	0	0	0	0
Pelagic	0	0	0	0	0.14	0.33

Note: Only traits contributing at least once to turnover are shown.

Marenzelleria at both sites (Cochran–Mantel–Hanenszel statistic = 11.6, $P = 0.0206$; CMH = 12.37, $P = 0.0148$ for the shallow and deep site, respectively). At the deep site there were three distinct time periods (Appendix S1: Fig. 1a). Before the invasion of *Marenzelleria* in the 1990s, the community was dominated by taxa that lived for 2–3 yr, while during the arrival period (1990–2004) taxa with longevity of 5–10 yr dominated. After *Marenzelleria* had established (2005–2011), the community was again dominated by taxa that lived for 2–3 yr. The shallow site was dominated by taxa that lived for 2–3 yr before 1990 and dominated by taxa that lived for 5–10 yr after this time.

There was not so strong an effect for size structure at either site with $P = 0.0824$ (CMH = 6.69) at the deep and $P = 0.0943$ (CMH = 6.36) at the shallow site (Appendix S1: Fig. 1b). There was no significant difference associated with the invasion in feeding type at either site (CMH = 6.43, $P = 0.1690$ (deep); CMH = 6.90, $P = 0.1413$ (shallow)), with surface deposit feeders always being dominant (Appendix S1: Fig. 1c). There was also no strong significant difference in sediment mixing/stabilizing categories (CMH = 8.29, $P = 0.0875$; CMH = 5.95, $P = 0.0509$ at the deep and shallow site, respectively). However, it seemed that decreasing abundance of biodiffusers and increasing abundance of gallery diffusion occurred at both sites, coincident with the invasion of *Marenzelleria,* until gallery diffusion was the dominant trait at the deep site by 2004 (Appendix S1: Fig. 1d).

Question 3

Traits associated with *Marenzelleria* did not affect functional turnover in a random fashion at either site or for either time period (arrival or established). At the deep site, nonrandomness was observed for both time periods ($P = 0.080$, $P = 0.075$ for arrival and established periods, respectively), but at the shallow site, nonrandomness was more obvious during the arrival time period ($P < 0.001$ *cf.* $P = 0.025$).

DISCUSSION

Our results did not support our hypotheses on the effects of the arrival and establishment of an invasive species. No reduction in taxa richness occurred with the advent of the invasion and no statistically significant change in taxa turnover was observed at one site while a significant increase was observed at the other. While number of traits increased with the invasion, this was only detected at one site and was accompanied by a decrease in trait turnover. Despite this, the functional traits exhibiting turnover changed nonrandomly with the invasion, suggesting that species additions and removals do have the potential to affect functional redundancy.

There is ongoing scientific debate as to whether homogenization and reduction in species diversity related to invasives is due to the invasion or the habitat alteration (often homogenization) which allows successful invasion to occur (Moyle and Light 1996, Gurevitch and Padilla

2004, Clark et al. 2013). In soft-sediment systems, bioturbators like *Marenzelleria* create a habitat that often has less species diversity than other habitats due to sediment destabilization (Widdicombe et al. 2000, Lohrer et al. 2008, de Juan and Hewitt 2011). Despite this, we observed an increase in taxa richness at both sites and an increase in turnover at the shallow site. While increased extinction probabilities or emigration rates of native species could lead to increased species turnover with invasion, this should be accompanied by a decrease in taxa richness, which we did not observe.

The responses of taxa and functional trait turnover were disjunctive, with trait turnover decreasing after the invasion at one site and taxa turnover increasing at the other. This disjunctive response led to the correlation between trait and taxa turnover changing from being a strong positive correlation at both sites prior to 1991 (Spearman's ϱ = 0.87 and 0.88 at the deep and shallow sites respectively), to being increasingly less well correlated (deep site, Spearman's ϱ = 0.60 and 0.54; and shallow site, Spearman's ϱ = 0.52 and 0.30 in the arrival and established periods, respectively). As relative differences between species and trait diversity have been used to determine community assemblage processes (Pavoine and Bonsall 2011, Spasojevic and Suding 2012), this may suggest that at our sites a change has occurred over time in how the communities assemble. In fact, when *Monoporeia* was dominant, the community was generally not composed of larval dispersers, while taxa coexisting with *Marenzelleria* were, suggesting the potential for a major switch in metacommunity properties over time. However, decreasing trait turnover over time unaccompanied by decreasing taxa turnover has also been suggested as an indicator of the importance of initial community composition (historical context, Fukami et al. 2005). Our study may support this view as we observed this at the deep site, where *Monoporeia* (the previous dominant) had higher densities and a 1920s community very different from the other time periods.

It seems likely that the increase in taxa turnover observed at both sites, although only statistically significant at one, was actually associated with a marked decline in abundance of the dominant species (*Monoporeia affinis*) which occurred prior to the invasion. At the shallow site, this decline was a sharp drop over a few years, while at the deep site the decline was more gradual. Taxa turnover was low (lower than generally reported (Magurran and Henderson 2010, Manukau Harbor New Zealand Hewitt pers. comm.) until 1988–1989 when a marked increase in both the maximum and minimum turnover lifted the turnover range to that similar to other reported ranges. This increase occurred at both sites, coincident with the decline in *Monoporeia* abundances (to 700–900 individuals/m^2) and an increase in the abundance of *Macoma balthica*. *Monoporeia* is reputed to prey on *Macoma* larvae and to be more sensitive to high temperatures than *Macoma* (Segerstrale 1957, Beukema et al. 2009). Rousi et al. (2013) suggest that rising surface temperatures triggered a decline in *Monoporeia* allowing *Macoma* to increase in abundance to levels seen in a previous period of higher temperatures (the 1920s).

Thrush et al. (2009) suggest that central to the resilience of a community is whether key species are sensitive to the changes occurring. Many of the variations we observed seem to be driven by changes in abundance of three key species; even the success of the invader may be a response to other strong disturbances in the system. Present research highlights all the following disturbances occurring in the Baltic, climatic changes, including temperature (Rousi et al. 2013) and duration and the thickness of ice cover (Merkouriadi and Leppäranta 2014), and potential regime shifts based on climatic factors and fishing pressure (Österblom et al. 2007, Möllmann et al. 2009).

Despite the varying responses observed between the two sites, our results do raise some interesting points. The very lack of strong consistent responses suggest that effects of invasives are not only system- and species-dependent (Strayer et al. 2006), but also depend on community dynamics, in particular the assembly processes (Davis 2003), and historical context. Metacommunity theory provides the framework and the methods to determine the mechanisms behind how specific communities are assembled and the role dispersal and other functional traits play in their maintenance (Heino et al. 2015). Understanding the specific mechanism(s) assembling the community may hold the key to providing generalities underlying invasion effects. However, a major challenge for ecologists is understanding

when species identity and the specific traits displayed by dominant or key species become necessary for understanding community dynamics and resilience to change, whether it be environmental or biotic driven.

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Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.1289/supinfo