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

Hewitt, Judi E.

2016-03

Hewitt, J. E., Norkko, J., Kauppi, L., Villnäs, A & Norkko, A. 2016, 'Species and functional trait turnover in response to broad-scale change and an invasive species ' Ecosphere, vol. 7, no. 3, 01289. https://doi.org/10.1002/ecs2.1289

http://hdl.handle.net/10138/176229
https://doi.org/10.1002/ecs2.1289

Downloaded from Helda, University of Helsinki institutional repository.
This is an electronic reprint of the original article.
This reprint may differ from the original in pagination and typographic detail.
Please cite the original version.
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., re-
duce both species richness and turnover; Gordon 
1998, Claver et al. 2009). This reduction in spe-
cies richness may vary with length of time since 
invansion (Strayer et al. 2006, Clark et al. 2013) and 
the background diversity of the system invaded 
(Villnäs and Norkko 2011). Following these gen-
eralities, species turnover would also be expected 
to vary with invasion, increasing as native spe-
cies 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 compar-
ing 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 di-
versity are reported to reflect differing commu-
nity 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 commu-
nities 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 dif-
ficult to predict the generalities of trait diversity 
responses to change from studies on taxonomic 
responses.

Temporally, functional trait composition of for-
est communities changes faster than expected af-
after acute disturbances (Swenson et al. 2012), thus 
increasing functional turnover. Successful inva-
sive species are often expected to be functionally 
distinct (Vitousek 1996, Parker et al. 1999, Fargi-
one 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 diffi-
cult to predict. If niche-based assembly processes 
are driving functional turnover, the effects of ad-
dition 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 
comprising a limited number of benthic spe-
cies (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 possi-
ble 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 mid-
dle 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, high-
ly abundant member of the benthic communities 
(Kauppi et al. 2015). As the adult individuals of 
Marenzelleria tolerate stressful hypoxic condi-
tions and generally live deeper in the sediments 
than the native species, it is potentially filling a 
vacant niche in the system (Leppäkoski and Ole-
nin 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 partic-
ular, 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 inclu-
sion 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 cm²), 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-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, 1–2, 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 \( \frac{\gamma}{\alpha} - 1 \) (Whittaker 1960) on presence/absence of data between pairs of subsequent years (where \( \gamma \) is the total number of taxa found in both years and \( \alpha \) 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
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
before period (KW = 8.83, $P = 0.0121$), but trait
turnover increased when *Marenzelleria* spp. ar-
ribed, with trait turnover highest in the before
period (KW = 6.31, $P = 0.0425$).
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
Marenzelleria at both sites (Cochran–Mantel–Haenszel 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 diffuser 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

| Traits                  | Deep site Before | Deep site Arrival | Deep site Established | Shallow site Before | Shallow site Arrival | Shallow site 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.*
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 $\rho = 0.87$ and 0.88 at the deep and shallow sites respectively), to being increasingly less well correlated (deep site, Spearman’s $\rho = 0.60$ and 0.54; and shallow site, Spearman’s $\rho = 0.52$ and 0.30 in the arrival and established periods, respectively). As relative differences between species and trait diversity have been used to determine community assembly 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.

**Acknowledgments**

Funding for this manuscript was obtained from: the Walter and Andrée De Nottbeck Foundation senior fellowship to JEH in 2013; from NIWA’s Coasts and Oceans Centre (JEH); the University of Helsinki (3-yr grant to JN); the BONUS COCOA-project supported by BONUS (Art 185), funded jointly by the EU and the Academy of Finland; and the Maj and Tor Nessling Foundation (Grant no. 2014322). The manuscript was improved by the comments of an anonymous reviewer and the subject editor.

**Literature Cited**

Beukema, J., R. Dekker, and J. Jansen. 2009. Some like it cold: populations of the tellinid bivalve *Macoma balthica* (L.) suffer in various ways from a warming climate. Marine Ecology Progress Series 384:135–145.

Bonsdorff, E. 2006. Zoobenthic diversity-gradients in the Baltic Sea: continuous post-glacial succession in a stressed ecosystem. Journal of Experimental Marine Biology and Ecology 330:383–391.

Bremner, J. 2008. Species’ traits and ecological functioning in marine conservation and management. Journal of Experimental Marine Biology and Ecology 366:37–47.

Buendia, C., C. N. Gibbins, D. Vericat, and R. J. Batalla. 2014. Effects of flow and fine sediment dynamics on the turnover of stream invertebrate assemblages. Ecohydrology 7:1105–1123.

Carstensen, J., D. J. Conley, E. Bonsdorff, B. G. Gustafsson, S. Hietanen, U. Janas, T. Jilbert, A. Maximov, A. Norkko, and J. Norkko. 2014. Hypoxia in the Baltic Sea: biogeochemical cycles, benthic fauna, and management. Ambio 43:26–36.

Clark, G. F., E. L. Johnston, and B. Leung. 2013. Intrinsic time dependence in the diversity–invasibility relationship. Ecology 94:25–31.

Clarke, R. T., and R. N. Gorley. 2006. Primer v6. Primer-e, Plymouth, UK.

Clavero, M., L. Brotons, P. Pons, and D. Sol. 2009. Prominent role of invasive species in avian biodiversity loss. Biological Conservation 142:2043–2049.

Davis, M. 2003. Biotic globalization: does competition from introduced species threaten biodiversity? BioScience 53:481–489.

de Juan, S., and J. Hewitt. 2011. Relative importance of local biotic and environmental factors versus regional factors in driving macrobenthic species richness in intertidal areas. Marine Ecology Progress Series 423:117–129.

de Juan, S., S. F. Thrush, and J. E. Hewitt. 2013. Counting on β-diversity to safeguard the resilience of estuaries. PLoS ONE 8:e65575.

Fargione, J., C. S. Brown, and D. Tilman. 2003. Community assembly and invasion: an experimental test of neutral versus niche processes. Proceedings of the National Academy of Sciences USA 100:8916–8920.

Fukami, T., T. Martijn Bezemer, S. R. Mortimer, and W. H. van der Putten. 2005. Species divergence and trait convergence in experimental plant community assembly. Ecology Letters 8:1283–1290.

Gordon, D. R. 1998. Effects of invasive, non-indigenous plant species on ecosystem processes: lessons from Florida. Ecological Applications 8:975–989.

Gurevitch, J., and D. K. Padilla. 2004. Are invasive species a major cause of extinctions? Trends in Ecology & Evolution 19:470–474.

Heino, J., A. S. Melo, T. Siqueira, J. Soininen, S. Valanko, and L. M. Bini. 2015. Meta-community organisation, spatial extent and dispersal in aquatic systems: patterns, processes and prospects. Freshwater Biology 60:845–869.

Hewitt, J. E., S. F. Thrush, and P. D. Dayton. 2008. Habitat variation, species diversity and ecological functioning in a marine system. Journal of Experimental Marine Biology and Ecology 366:116–122.

Hietanen, S., A. O. Laine, and K. Lukkari. 2007. The complex effects of the invasive polychaetes *Marenzelleria* spp. on benthic nutrient dynamics. Journal of Experimental Marine Biology and Ecology 352:89–102.

Hughes, A. R., J. E. Byrnes, D. L. Kimbro, and J. J. Stachowicz. 2007. Reciprocal relationships and potential feedbacks between biodiversity and disturbance. Ecology Letters 10:849–864.

Josefson, A. B., J. Norkko, and A. Norkko. 2012. Burial and decomposition of plant pigments in surface sediments of the Baltic Sea: role of oxygen and benthic fauna. Marine Ecology Progress Series 455:33–49.

Kauppi, L., A. Norkko, and J. Norkko. 2015. Large-scale species invasion into a low-diversity system: spatial and temporal distribution of the invasive polychaetes *Marenzelleria* spp. in the Baltic Sea. Biological Invasions 17:2055–2074.

Leppäkoski, E., and S. Olenin. 2000. Non-native species and rates of spread: lessons from the brackish Baltic Sea. Biological Invasions 2:151–163.
Lohrer, A. L., L. D. Chiaroni, J. E. Hewitt, and S. F. Thrush. 2008. Biogenic disturbance determines invasion success in a subtidal soft-sediment system. Ecology 89:1299–1307.

Magurran, A. E., and P. A. Henderson. 2010. Temporal turnover and the maintenance of diversity in ecological assemblages. Philosophical Transactions of the Royal Society B 365:3611–3620.

Mason, N. W. H., and F. de Bello. 2013. Functional diversity: a tool for answering challenging ecological questions. Journal of Vegetation Science 24:777–780.

Merkouriadi, I., and M. Leppäranta. 2014. Long-term analysis of hydrography and sea-ice data in Tvärminne, Gulf of Finland, Baltic Sea. Climatic Change 124:1–11.

Möllmann, C., R. Diekmann, B. Müller-Karulis, G. Kor-nilovs, M. Plikshs, and P. Axe. 2009. Reorganization of a large marine ecosystem due to atmospheric and anthropogenic pressure: a discontinuous regime shift in the Central Baltic Sea. Global Change Biology 15:1377–1393.

Mouillot, D., S. Spatharis, S. Reizopoulou, T. Laugier, L. Sabetta, A. Basset, and T. Do Chi. 2006. Alternatives to taxonomic-based approaches to assess changes in transitional water communities. Aquatic Conservation: Marine and Freshwater Ecosystems 16:469–482.

Mouillot, D., N. A. J. Graham, S. Villéger, N. W. H. Mason, and D. R. Bellwood. 2013. A functional approach reveals community responses to disturbances. Trends in Ecology & Evolution 28:167–177.

Moyle, P. B., and T. Light. 1996. Fish invasions in California: do abiotic factors determine success? Ecology 77:1666–1670.

Norkko, E., E. Bonsdorff, and C. Boström. 1993. Observations of the polychaete Marenzelleria viridis (Ver-ril) on a shallow sandy bottom on the south coast of Finland. Memoranda Societas pro Fauna Flora Fennica 69:112–113.

Norkko, J., D. C. Reed, K. Timmermann, A. Norkko, B. G. Gustafsson, E. Bonsdorff, C. P. Slomp, J. Carstensen, and D. J. Conley. 2012. A welcome can of worms? Hypoxia mitigation by an invasive species. Global Change Biology 18:422–434.

Norkko, A., A. Villnäs, J. Norkko, S. Valanko, and C. Pilditch. 2013. Size matters: implications of the loss of large individuals for ecosystem function. Scientific Reports 3:2646.

Österblom, H., S. Hansson, U. Larsson, O. Hjerne, F. Wulf, R. Elmgren, and C. Folke. 2007. Human-induced trophic cascades and ecological regime shifts in the Baltic Sea. Ecosystems 10:877–889.

Parker, I. M., D. Simberloff, W. Lonsdale, K. Goodell, M. Wonham, P. Kareiva, M. Williamson, B. Von Holle, P. Moyle, and J. Byers. 1999. Impact: toward a framework for understanding the ecological effects of invaders. Biological Invasions 1:3–19.

Pavoine, S., and M. B. Bonsall. 2011. Measuring biodiversity to explain community assembly: a unified approach. Biological Reviews 86:792–812.

Quintana, C. O., T. Hansen, M. Delefosse, G. Banta, and E. Kristensen. 2011. Burrow ventilation and associated porewater irrigation by the polychaete Marenzelleria viridis. Journal of Experimental Marine Biology and Ecology 397:179–187.

Renz, J. R., and S. Forster. 2013. Are similar worms different? A comparative tracer study on bioturbation in the three sibling species Marenzelleria arctica, M. viridis, and M. neglecta from the Baltic Sea. Limnology and Oceanography 58:2046–2058.

Rousi, H., A. O. Laine, H. Peltonen, P. Kangas, A.-B. Andersin, J. Rissanen, E. Sandberg-Kilpi, and E. Bonsdorff. 2013. Long-term changes in coastal zoo-benthos in the northern Baltic Sea: the role of abiotic environmental factors. ICES Journal of Marine Science: Journal du Conseil 70:440–451.

Segerstrale, S. G. 1957. Baltic Sea. Geological Society of America Memoirs 67:751–800.

Siefert, A., C. Ravenscroft, M. D. Weiser, and N. G. Swenson. 2013. Functional beta-diversity patterns reveal deterministic community assembly processes in eastern North American trees. Global Ecology and Biogeography 22:682–691.

Spassojevic, M. J., and K. N. Suding. 2012. Inferring community assembly mechanisms from functional diversity patterns: the importance of multiple assembly processes. Journal of Ecology 100:652–661.

Statzner, B., S. Dolédec, and B. Hugueny. 2004. Biological trait composition of European stream invertebrate communities: assessing the effects of various trait filter types. Ecography 27:470–488.

Stigzelius, J., A. Laine, J. Rissanen, A.-B. Andersin, and E. Ilus. 1997. The introduction of Marenzelleria viridis (Polychaeta, Spionidae) into the Gulf of Finland and the Gulf of Bothnia (northern Baltic Sea). Annales Zoologici Fennici 34:205–212.

Strayer, D. L., V. T. Eviner, J. M. Jeschke, and M. L. Pace. 2006. Understanding the long-term effects of species invasions. Trends in Ecology & Evolution 21:645–651.

Swenson, N. G., P. Anglada-Cordero, and J. A. Barone. 2011. Deterministic tropical tree community turnover: evidence from patterns of functional beta diversity along an elevational gradient. Proceedings of the Royal Society B: Biological Sciences 278:877–884.

Swenson, N. G., et al. 2012. Temporal turnover in the composition of tropical tree communities: functional determinism and phylogenetic stochasticity. Ecology 93:490–499.
Tanentzap, A. J., W. G. Lee, and K. A. C. Schulz. 2013. Niches drive peaked and positive relationships between diversity and disturbance in natural ecosystems. Ecosphere 4:art133.

Thrush, S. F., J. E. Hewitt, P. K. Dayton, G. Coco, A. M. Lohrer, A. Norkko, J. Norkko, and M. Chiantore. 2009. Forecasting the Limits of Resilience: Integrating Empirical Research with Theory Proceedings of the Royal Society B 276:3209–3217.

Villnäsi, A., and A. Norkko. 2011. Benthic diversity gradients and shifting baselines: implications for assessing environmental status. Ecological Applications 21:2172–2186.

Villnäsi, A., J. Norkko, K. Lukkari, J. Hewitt, and A. Norkko. 2012. Consequences of increasing hypoxic disturbance on benthic communities and ecosystem functioning. PLoS ONE 7:e44920.

Vittousek, P. M. 1990. Biological invasions and ecosystem processes: towards an integration of population biology and ecosystem studies. Pages 183–191 in Samson, F. B., and F. L. Knopf, editor. Ecosystem management. Springer-Verlag, New York, New York, USA.

Whittaker, R. H. 1960. Vegetation of the Siskiyou mountains, Oregon and California. Ecological Monographs 30:279–338.

Widdicombe, S., M. C. Austen, M. A. Kendall, R. M. Warwick, and M. B. Jones. 2000. Bioturbation as a mechanism for setting and maintaining levels of diversity in subtidal macrobenthic communities. Hydrobiologia 440:369–377.

**Supporting Information**

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