Zostera marina seagrass meadows as a model for the consequences of genetic diversity at the ecosystem level

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Abstract

While much work has been done to establish the consequences of species level loss for ecosystem function, comparatively little research has been done to establish a link between genetic diversity and ecosystem level functions. The last decade has seen a small body of research accumulate on the impacts of genetic diversity on responses to ecosystem disturbances in seagrass ecosystems based on the primary producer species *Zostera marina*. This research seems to indicate that a positive correlation exists between increased levels of genetic diversity and rate of recovery from various types of disturbance. A positive link is also demonstrated between periods of recovery in genetically diverse plots and increases in abundance of fauna dependent on *Z. marina*. While this research is of value as a starting block from which to launch further studies, the reliance of these studies upon neutral microsatellite sequences to assess levels of genetic diversity reduces the validity of the assumptions that can be made based upon these models. This is due to a lack of connection between neutral markers and phenotypes capable of influencing ecosystem level responses to disturbance.

Keywords

Ecosystem function, ecosystem genetics, eelgrass, microsatellites, resilience.

Introduction

While exact data concerning rates of loss of biodiversity are a topic of debate in the biological and ecological sciences (Stork, 2010), it is largely accepted that increased rates of biodiversity loss as a result of anthropogenic factors and climate change (arguably also anthropogenic) are a reality (Flannery, 2010). While there is a growing body of research that focuses on loss at the species level and its negative consequences for ecosystem stability and productivity (Fox & Harpole, 2008; Reusch & Hughes, 2006), comparatively little work has been done on the role of genetic diversity effects at the ecosystem productivity especially in the face of ecosystem disturbance (A. R. Hughes, Inouye, Johnson, Underwood,

& Vellend, 2008). While some ecosystems are quite diverse at the species level, warranting research at this scale, many other ecosystems are less species rich and reliant upon a single dominant species, these species often being primary producers that provide not only food for species at higher trophic levels but shelter as well (Reusch, Ehlers, Hammerli, & Worm, 2005).

Zostera marina meadows are an example of this type of ecosystem and have served as a model for the work of several groups of researchers who have attempted to explore the implications of various levels of genetic diversity on the ability of these ecosystems to recover from disturbance. This review shall first provide an overview of why *Zostera marina* is a suitable choice as a representative model for ecosystems dominated by a single primary producer species. Following this a summary of the findings of the principle pieces of research that have focused on genetic diversity in these ecosystems shall be given. The implications of this research for ecology and conservation in a wider sense shall be explored also before finally, an analysis of the problems with these models will be performed along with suggestions for how future research could address these problems.

***Zostera marina*: a primary producer of scientific interest**

Z. marina, colloquially known as 'eelgrass', is a monoecious variety of seagrass that is the dominant macrophyte species in many seagrass meadow ecosystems (Reusch et al., 2005). Though declining, this seagrass is still widely distributed along the coastlines of the northern hemisphere, making it and the ecosystems it supports convenient objects of study (Larkum, Orth, & Duarte, 2006). In addition, *Z. marina* primarily appears in clonal monoculture making experimental studies of genetic diversity relatively simple as genotypes are not overly varied and interference from other species can be largely ruled out, not only in experimental plots but in naturally occurring meadows (A. R. Hughes et al., 2008). While relatively little is known about *Z. marina* in terms of genetics when compared to other seagrass species (Larkum et al., 2006), enough is known to make use of DNA microsatellite markers via polymerase chain reaction (PCR) in studies of genetic diversity (Ehlers, Worm, & Reusch, 2008; A. Hughes & Stachowicz, 2004, 2011; A. R. Hughes et al., 2008; Reusch et al., 2005). In terms of the function of this species within its ecosystem, *Z. marina* is an important primary producer that; plays an important role in its food web, stabilises the seabed in which it grows (reducing turbidity), creates a complex environment in which other species can thrive and serves as a habitat for commercially important species such as flounder, cod and scallops (Larkum et al., 2006). The importance of these ecosystems as commercial commodities was proven when eelgrass was lost in two estuarine lagoons in Japan in the 1950s resulting in the total collapse of the fishing economy of town that relied upon one of these water bodies (Yamamuro, Hiratsuka, Ishitobi, Hosokawa, & Nakamura, 2006). The combination of all of these factors make these seagrass ecosystems both a convenient and important choice for studies of the role of genetic diversity in the stability of ecosystems.

The role of genetic diversity in *Zostera marina* meadows: research findings

Several pieces of research have provided evidence of the importance of genetic diversity in eelgrass meadow based ecosystems, particularly with regard to the ability of these ecosystems to withstand and recover from disturbances both natural and experimental. Research carried out over 2002-2003 based on the laying of plots of *Z. marina* with controlled numbers of genotypes present (determined by microsatellites) ranging from one to eight genotypes, revealed that after grazing by migrating geese the plots with the greatest genetic diversity returned to near pre-grazing shoot densities more rapidly than those with less genotypes present (Fig. 1) (A. Hughes & Stachowicz, 2004). A point of interest is that invertebrate abundance also increased on a per shoot basis following disturbance (A. Hughes & Stachowicz, 2004). Taken together, this can be considered evidence of genetic diversity being important for the consistency and reliability of this ecosystem following a natural disturbance.

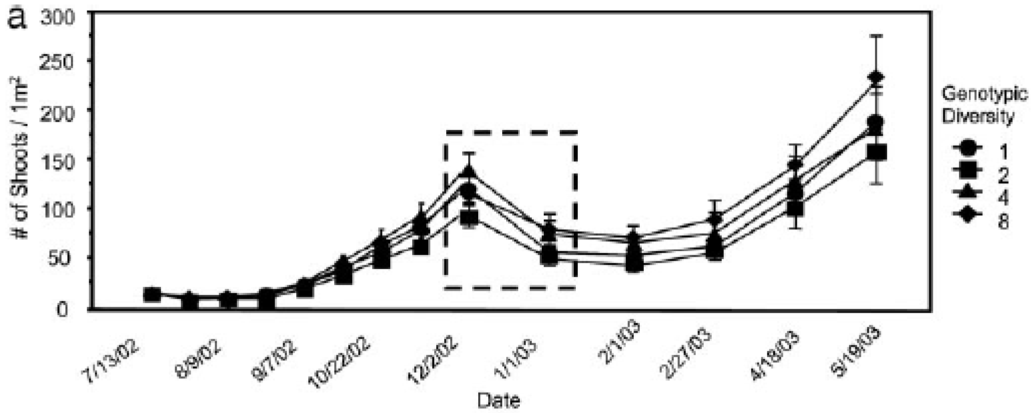

Fig. 1. Shoot densities in *Zostera marina* by date for plots with genetic diversity indicated.

Adapted from Hughes & Stachowicz, 2004, p. 9000.

Other eelgrass based research carried out over a period of extreme warming in Europe in 2003 also suggests that genetic diversity has positive effects for these ecosystems in the face of disturbance (Reusch et al., 2005). Similarly to the work described prior, this experiment involved plots with set numbers of measured genotypes, in this case one, three and six genotypes based on microsatellite markers, as well as monoculture plots of each genotype (Reusch et al., 2005). The research results showed a clear pattern of increased plant density, productivity and faunal abundance, despite raises in temperature that were potentially damaging to these ecosystems, in plots with higher levels of genetic diversity (Fig. 2) (Reusch et al., 2005). The increased faunal abundance is a good indicator of the positive correlation that may exist between genetic diversity in a primary producer and the ecosystem this species supports.

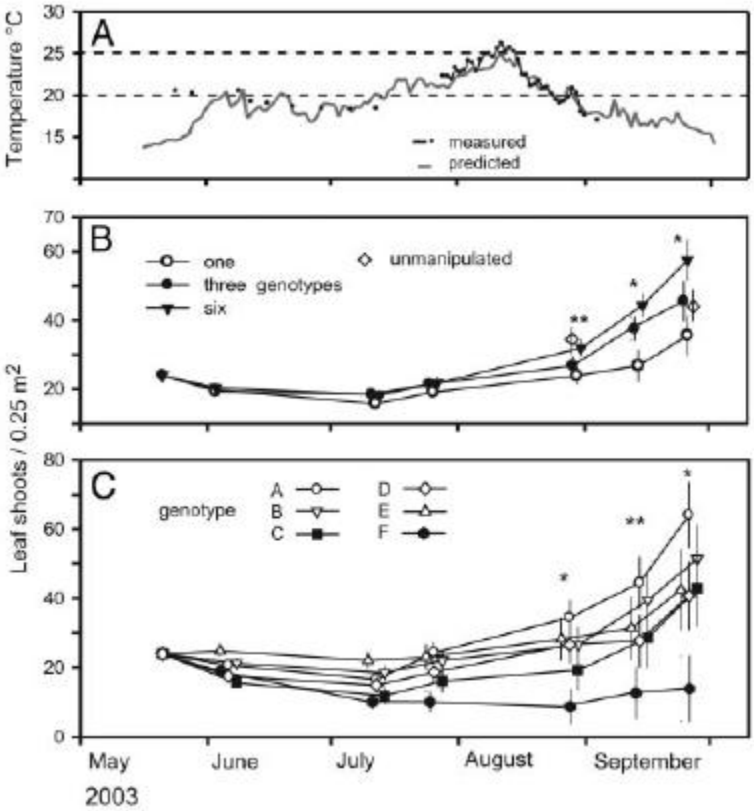

Fig. 2. Shoot densities in *Zostera marina* by genotype number, or monoculture plot, in relation to temperature.

Adapted from Reusch, Ehlers, Hammerli & Worm, 2005, p. 2827.

Further research was carried out by Reusch et al in 2004 in following with that described above. In this further experiment, plots of seagrass with similarly selected variations of genotypes were planted in tanks where warming could be controlled experimentally and compared with control tanks with normal water temperatures (Ehlers et al., 2008). The authors concluded that while warming was harmful overall to these eelgrass plots, genotypic diversity provided a buffer against these effects as was theorised after their earlier work (Ehlers et al., 2008). That genetic diversity in this species seems to be positively correlated with resilience to warming is of importance when considering current thought on global warming and may be of consequence to other primary producer dependent ecosystems.

Between 2005 and 2007, a series of experiments were carried out by Hughes & Stachowicz to further explore the relationship between genetic diversity in *Z. marina* and the rate of recovery from disturbance established in their earlier work (A. Hughes & Stachowicz, 2011). These utilised genotypes as identified by five microsatellite markers specific to *Z. marina* (A. Hughes & Stachowicz, 2011). These experiments involved controlled clipping of shoots to simulate grazing and the observation of the effects of a naturally occurring macroalgal bloom (A. Hughes & Stachowicz, 2011). The controlled clipping experiment showed a greater increase in shoot density over two years in the plots with multiple genotypes than those with a single genotype (Fig. 3), reinforcing the conclusions they came to after observing the effects of grazing geese (described earlier) (A. Hughes & Stachowicz, 2011). Interestingly, differences in shoot density did not greatly differ among genetically diverse plots and monoculture plots in the presence of the macroalgae, with all plots losing shoots until the end of the bloom where the plots with greater genetic diversity showed greater rates of recovery (A. Hughes & Stachowicz, 2011). This demonstrates that genetic diversity may have limits in its ability to impart resilience against some threats, though retaining positive effects with regard to recovery after these disturbances.

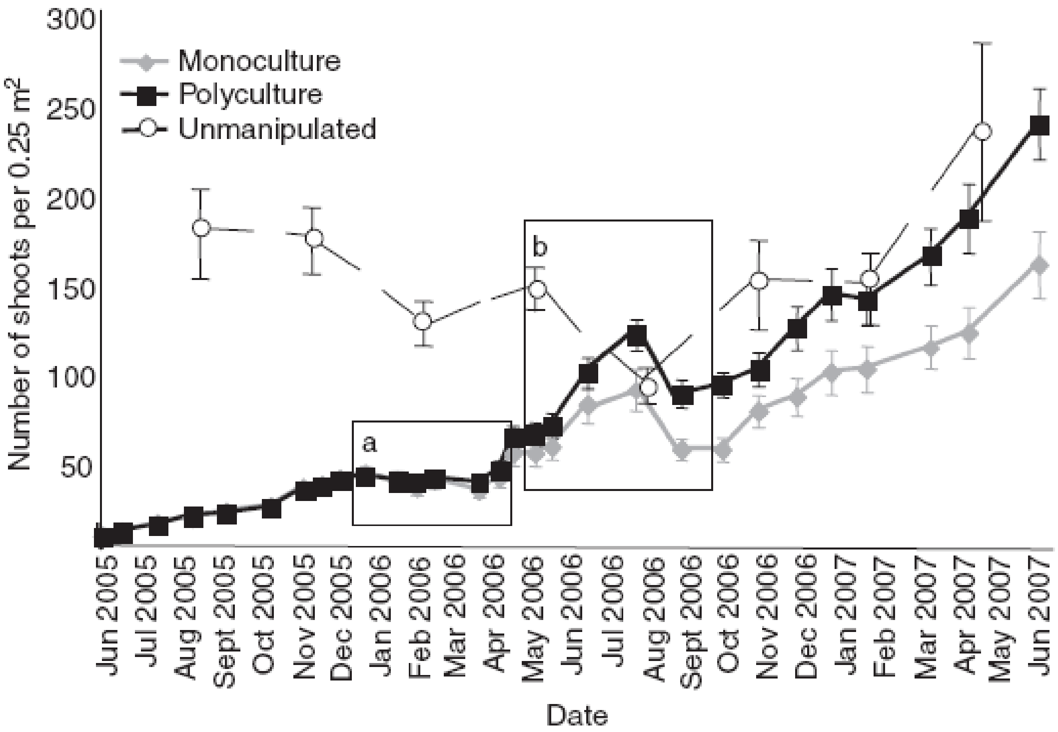

Fig. 3. Shoot densities per month in *Zostera marina* in monoculture, polyculture and unmanipulated plots.

Adapted from Hughes & Stachowicz, 2011, p. 448.

When synthesised, the results of the above experiments point to an important role for genetic diversity in the ability of this type of primary producer dependent ecosystem to re-proliferate following a period of disturbance, either natural or experimental. Of particular interest were the apparent increases in abundance of fauna dependent on these ecosystems following periods of disturbance. The results of the research analysed seem to suggest that genetic diversity can play a similar role to diversity at the species level in more complex ecosystems when considering response to disturbance (A. Hughes & Stachowicz, 2011).

Consequences of *Zostera marina* research findings for the science of ecology

The consequences of the eelgrass research described are not limited to the ecology, management and conservation of these ecosystems. As mentioned in the introduction, many ecosystems are dependent upon primary producer species for normal functioning.

These ecosystems include seagrass kelp forests, marshes and fir forests among others (A. Hughes & Stachowicz, 2004). With this in mind it is possible to theorise that similar importance can be placed on genetic diversity in these ecosystems.

While much research and conservation energy has been focused on the preservation of species level diversity, and with reason given the comparatively well understood effects of species diversity (Fox & Harpole, 2008), the seagrass focused research above may indicate that more attention should be given to the importance of genetic diversity in primary producers in order to balance our approach to ecosystem management and restoration. Studies of genetic diversity in more complex ecosystems may also yield further insight into how pressure upon one species in a given trophic level due to pathogens or anthropogenic factors can affect organisms living at other levels within this ecosystem (Schaberg, DeHayes, Hawley, & Nijensohn, 2008).

The significance of genetic diversity can also be applied to the important man-made ecosystems of agriculture, where research has also demonstrated a link between genetic diversity in crops and increased yield (A. R. Hughes et al., 2008). From a genetic science perspective, this research also shows the value of the PCR based tools we have acquired and been able to apply to ecological studies in the form of the amplification of microsatellite markers to assess levels of genetic diversity.

Problems with the *Zostera marina* models

There are three main problems with the *Z. marina* based models of genetic diversity and ecosystem resilience that could be identified. The first concerns how the genetic data has been used to reach the conclusions given by the research described. The second comes as a result of conflicting research data from another seagrass study based upon another species, *Posidonia oceanica*. The final problem lays in the fact that some bodies of research postulate that a lack of genetic diversity can also be beneficial for some species.

First, each of the research items described above has used PCR amplification of microsatellite sequences to generate its definition of genetic diversity. The problem with this model is that microsatellite markers are traditionally considered to be neutral and are thus not necessarily linked to phenotypes that are of consequence to the functioning of an ecosystem (A. R. Hughes et al., 2008). In order to be more conclusive, future studies should focus on genotypes known to produce certain phenotypes that can be observed and their effects measured.

Secondly, research undertaken on *Posidonia oceanic*a meadows has revealed that other factors may be more important for mortality in seagrass species than genetic diversity, such as rates of sedimentation (Arnaud-Haond, Marbà, Diaz-Almela, Serrão, & Duarte, 2010). In this study, genotypic diversity was also positively correlated with mortality in *P. oceanica*, in stark contrast with the *Z. marina* results described above (Arnaud-Haond et al., 2010). Future studies could perhaps make comparisons between various species of seagrass in order to rule out species specific effects.

Lastly, our understanding of the importance of genetic diversity in general is, at this stage, largely theoretical and reliant upon very specific pieces of research like those described. Research on arthropods and other social animals has suggested that a lack of genetic diversity can also have positive effects through increasing the likelihood of altruistic behaviour (Flannery, 2010). While this type of evolutionary behaviour based theory can't be applied directly to plants, it serves as an example of an effect of genetic diversity that runs counter to that postulated by the *Z. marina* based research, calling into question the universality of assumptions based on these results. Future research should aim to identify the circumstances under which greater levels of genetic diversity become more important for ecosystems.

Conclusion

Research projects based on *Z. marina* plots with controlled levels of genetic diversity have provided some positive links between genetic diversity and an ecosystem's ability to recover from a disturbance. In a time where loss of biodiversity as a result of anthropogenic actions (both direct and through climate change) is receiving a lot of attention, this research may provide clues as to how we can direct our focus in order to more effectively preserve and manage ecosystems that depend upon a dominant primary producer species. While the research is of value, it is not flawless, largely due to the limitations of genetic technology available to the researchers. Further work needs to be done to establish a concrete link between genetic diversity, beneficial phenotypes and ecological resilience before the patterns identified in the *Z. marina* studies become more widely accepted and applicable.

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