PERSPECTIVES IN ESTUARINE AND COASTAL SCIENCE

The Emerging Role of Genetic Diversity for Ecosystem Functioning: Estuarine Macrophytes as Models

Thorsten B. H. Reusch[1],* and A. Randall Hughes[2]

[1] *Max-Planck-Institute for Limnology, August-Thienemann-Strasse 2, 24306 Plön, Germany*
[2] *Section of Evolution and Ecology, One Shields Avenue, University of California, Davis, California 95616*

ABSTRACT: Recent experiments in macrophyte dominated communities on the relationship between biological diversity and ecosystem functioning suggest that effects and mechanisms of genetic-genotypic and species diversity are analogous. As previously shown for species diversity, genotypic diversity enhances ecosystem productivity and recovery from disturbance. These findings generalize ecological theory, and provide an empirical basis for explicitly considering the maintenance of genetic or genotypic diversity for conservation strategies. Macrophyte systems such as seagrasses or salt-marshes may be excellent systems to test the interaction between diversity across several (genetic versus species) levels of biological organization because they are relatively species poor while simultaneously allowing the manipulation of genotypic diversity by taking advantage of clonal propagation in many species.

Introduction

Biodiversity is hierarchically organized: genes make up genotypes and genotypes compose populations that collectively belong to species. Species themselves can be further grouped into functional groups, trophic levels, or ecological guilds that share common resource requirements or life histories. During the past decade, manipulative experiments have provided compelling evidence that biological diversity at multiple levels is important for ecosystem functioning and stability. In particular, diversity at the species and functional group level can enhance productivity, resistance and resilience in the face of disturbance, and stability with respect to temporal fluctuations (overview in Loreau et al. 2001; Loreau et al. 2002). The majority of biodiversity-ecosystem function studies have manipulated species richness in terrestrial grassland communities or experimental microcosms and mesocosms. At present, we have less understanding of the role of other levels of biodiversity and the interactions between them, and marine systems are clearly understudied (Emmerson et al. 2001; Stachowicz et al. 2002; Duffy et al. 2003).

This perspective addresses the emerging role of genetic diversity for ecosystem functioning and stability. For consistency with the majority of the literature (Vellend and Geber 2005), we will use the terminology diversity and richness (i.e., the number of species or genotypes) interchangeably. With ecosystem functioning we refer to primary and secondary production, energy transfer, and carbon storage. Important components of stability are resilience (time to return from disturbed state), resistance (resistance of the current state to disturbance), and variability (Pimm 1984). Traditionally species diversity and genetic diversity have been the focus of two separate fields, ecology and population genetics, respectively (Antonovics 1976; Vellend and Geber 2005). Genetic diversity may be particularly relevant ecologically in communities that are based on one or a few structuring species (ecosystem engineers sensu Jones et al. 1994), such as macrophyte-based aquatic communities that are locally dominated by a few species. Despite their low species diversity, salt marshes, seagrass meadows, and macroalgal beds represent some of the most productive and stable shallow water and estuarine ecosystems (Hemminga and Duarte 2000; Engelhardt and Ritchie 2001; Paine 2002; Travis and Hester 2005). The emerging consensus of a positive correlation between species diversity and ecosystem functioning (Loreau et al. 2001, 2002) cannot encompass these systems.

While macrophyte stands are apparently uniform at the level of structuring species, there are recent reports of high genetic-genotypic diversity in marsh

* Corresponding author; current address: Institute for Evolution and Biodiversity, University of Münster, Hüfferstr.1, 48149 Münster, Germany; tele: +49-251-83-21095; fax: +49- 251 83-24668; e-mail: treusch@uni-muenster.de

plants (Bockelmann et al. 2003; Travis and Hester 2005), seagrasses (Reusch et al. 2000; Procaccini et al. 2001; Olsen et al. 2004), and brown seaweeds (Coyer et al. 2003). With the development of highly variable deoxyribonucleic acid (DNA) based markers (Box 1), notably RAPD (rapid amplified polymorphic DNA), microsatellites, and AFLP (amplified fragment length polymorphism), these studies often reversed earlier reports of low genetic diversity in aquatic plants obtained by allozyme electrophoresis. In addition to enhancing our knowledge of genetic diversity in nonmodel organisms, these methodological advances now allow for precise manipulation of levels of genetic-genotypic diversity in experiments that specifically address the ecological function of genetic diversity.

A ROLE OF GENOTYPIC DIVERSITY FOR ECOSYSTEM FUNCTIONING: SEAGRASS BEDS AS MODEL SYSTEMS

Seagrasses, in particular, are excellent models for examining the ecological role of genetic diversity (see Duffy in press for a recent review of biodiversity-ecosystem function relationships in seagrasses). They form meadows that consist of one or only a few species (Hemminga and Duarte 2000) that perform a wide variety of functions typically associated with numerous species in other systems. The ecosystem services provided by these macrophyte stands in terms of nutrient fixation, erosion prevention, and nursery for commercial species are among the highest for all aquatic ecosystems (Costanza et al. 1997). Because seagrasses can reproduce clonally, they generate multiple shoots of the same genotype that can be manipulated in a manner analogous to individuals of different species in experiments of diversity and ecosystem function. Differences in resource use, rooting depth, or resistance to stress among plant genotypes could make more diverse seagrass meadows more productive and less vulnerable to disturbance.

Recent experiments using the widespread seagrass species *Zostera marina* (eelgrass) indicate that genotypic (or clonal) diversity may indeed replace the function of species diversity in ecosystems with few or a single foundation species. In an experiment in California by Hughes and Stachowicz (2004), mixtures of 1, 2, 4, and 8 eelgrass genotypes were planted into the intertidal zone of Bodega Bay. Diverse treatments lost fewer shoots due to the initial stress of transplantation and displayed greater resistance to the nearly destructive grazing by migrating brant geese (*Branta bernicla*) than monoculture plots. During the recovery period, diverse treatments had lower porewater nitrogen concentrations, suggesting greater resource utilization in these plots. The abundance (but not diversity) of associated invertebrates also increased, even on

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> ### Box 1: Widely Used Genetic Markers
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> Genetic markers are either random (i.e., the location on the chromosomes is undefined and indefinable) or specific. Widely used random markers are RAPD (Welsh et al. 1991) or AFLP (Bensch and Akesson 2005). While RAPD results are difficult to reproduce and to cross-standardize between labs, the AFLP technique allows for the reliable definition of hundreds of genetic polymorphisms even in non-model species without the need to develop specific Polymerase chain reaction (PCR)-primers (Bensch and Akesson 2005). DNA microsatellites (synonymous to short tandem repeats or simple sequence repeats) are sites on the DNA consisting of small motifs (2–6 nucleotides) that are repeated > 10 times (e.g., GAGAGAGAGAGAGAGAGAGA) and belong to specific markers that represent a single locus on the chromosome. Due to their rapid stepwise mutation rates, microsatellite loci typically display several length variants within populations (Ashley and Dow 1994). Such polymorphism can be used to distinguish individuals or to assess relatedness, mating patterns and genetic differentiation between populations. Microsatellites combine many useful features such as high abundance in all genomes, Mendelian inheritance, rapid genotyping through PCR based methods and high polymorphism. In molecular ecology and population genetics these advantages led to widespread and still growing application of anonymous microsatellites with an unknown location in the genome. Recently, abundant microsatellites have also been discovered in the immediate vicinity of expressed genes (gene-linked or type-1 microsatellites), prompting the question whether the general assumption of their selective neutrality is still tenable (Li et al. 2004). Such gene-linked microsatellites may be a novel class of markers that better reflect the genetic diversity for selectively relevant traits (van Tienderen et al. 2002).

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a standardized per shoot basis. These positive effects of diversity disappeared a few months after the grazing event, suggesting that the important role of genetic diversity may only be observed in response to stress or disturbance.

In the southwestern Baltic Sea (Germany), Reusch and colleagues combined a total of six genotypes into diversity treatments of 1, 3, and 6 genotypes (Reusch et al. 2005). Their experiment

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Box 2: Decomposition of Biodiversity Effects into Complementarity and Selection

Positive biodiversity effects may arise from different processes. As a statistically inevitable consequence, diverse communities are expected to contain the best performing species (or genotype, clone) within their mixture that may dominate the total response at termination. Whether or not such a sampling (or selection) effect can legitimately be attributed to biodiversity per se is controversial. On the other hand, true biodiversity effects arise when the average performance of species is enhanced by the presence of other species (or genotypes), e.g., through facilitation or niche differentiation. Loreau and Hector (2001) developed a statistical procedure that allows a decomposition of the net biodiversity effect into complementarity and selection effects. Based on appropriate experimental designs, the relative roles of complementarity versus selection can be disentangled provided that all species tested in mixtures are also present as experimental monocultures. Fox (2005) has recently expanded the approach of Loreau and Hector (2001). Net biodiversity effects are decomposed into three components, trait-dependent complementarity, trait-independent complementarity, and dominance, the latter being equivalent to natural selection. The above procedures can also be adapted for genotypic instead of species diversity (Reusch et al. 2005).

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coincided with a period of extreme water temperatures caused by the unparalleled heat wave that hit Europe in 2003 (Schär et al. 2004). The temperature conditions in 2003 can be viewed as an uncontrolled experiment, simulating conditions of predicted global warming in coming decades. Similar to the response in the Californian experiment, the more diverse assemblages of eelgrass genotypes showed faster recovery after the summer mortality. There also were more shoots, biomass, and associated invertebrates in diverse plots at the end of the experiment.

In the experiment conducted by Reusch and coworkers, all genotypes tested in mixtures were also transplanted as monocultures. This way, positive biodiversity effects could be dissected into complementarity and selection (see Box 2). The analysis revealed that true biodiversity effects through complementarity were responsible for the enhanced performance of diverse treatments, con-

firming qualitative observations by Hughes and Stachowicz (2004). Selection effects were negative, suggesting that genotypes performing well in monoculture grew below average in mixtures (Reusch et al. 2005).

Does genotypic diversity in seagrass beds only play a role under stress or disturbance, as the only two available studies in eelgrass beds suggest? A controlled tank experiment conducted in 2004 to simulate the 2003 heat wave indicates that genotypic diversity is important in both stressed and non-stressed conditions (Ehlers et al. unpublished data). Additional tests in the field are highly warranted that manipulate frequency and type of disturbance fully crossed with genetic-genotypic diversity. The spatial scale at which experiments were conducted so far was limited to the classical plot size of 1×1 m. We need to scale up in order to examine whether local benefits of genetic diversity (Hughes and Stachowicz 2004; Reusch et al. 2005) or variation between populations (Hilborn et al. 2003) result in enhanced ecosystem performance at an estuarine or bay-wide level.

GENETIC VERSUS GENOTYPIC DIVERSITY

Experiments so far have manipulated the level of genotypic diversity (i.e., the number of distinct clones per area). In doing so, such experiments are analogous to manipulation of species diversity (or richness) and are a sensible starting point (Vellend and Geber 2005). The next logical question to investigate is the effect of the aggregate genetic diversity among a collection of genotypes in an area or population (e.g., the degree of homozygosity at the level of individuals or the amount of inbreeding within populations). While widespread among animals and plants (David 1998), the relevance of correlations between marker heterozygosity and fitness are controversial (David 1998; Balloux et al. 2004). Notwithstanding, in eelgrass, there is evidence for better performance and higher Darwinian fitness in more heterozygous genotypes (heterozygote advantage; Williams 2001; Hämmerli and Reusch 2003). The importance of such findings for population growth and persistence in seagrasses, and in plant populations in general, is currently unclear (Montalvo et al. 1997). We do not know whether excess homozygosity documented in some seagrass populations translates to reduced population growth or resilience (Procaccini and Piazzi 2001).

A third aspect of genetic diversity that warrants investigation involves the genetic basis and population-level diversity of ecologically important traits. To experimentally address this relationship, one could quantify the reaction norm of genotypes in a quantitative genetic approach under a range of ecological challenges (Lynch 1996). Based on

a similarity matrix, test populations with different ranges of phenotypic diversity could then be composed. Given the high logistical effort for preparing the main diversity experiment, such an approach is hardly feasible. Conventional neutral genetic markers, such as anonymous microsatellites or AFLP (box 1), are not suitable, because the correlation between marker diversity and trait diversity is often weak at best (Lynch 1996; Milligan et al. 1994). An alternative is the development of a new generation of gene-linked markers, such as transcribed microsatellites (Woodhead et al. 2005) or single-nucleotide polymorphisms within genes (Morin et al. 2004). Ideally, the diversity of these markers will reflect selectively relevant traits (van Tienderen et al. 2002), allowing a rapid screening of populations for genetic surrogates of traits that are particularly relevant in the face of a defined ecological challenge (Luikart et al. 2003). Experiments could then be designed that compare populations of rather similar genotypes with those that consist of highly divergent genotypes.

GENETIC-GENOTYPIC VERSUS SPECIES DIVERSITY

The relative roles of species and genotypic-genetic diversity in ecosystem function are elusive at the moment. Evidence from terrestrial systems suggests that species diversity and genetic diversity are positively correlated (Booth and Grime 2003), but current evidence does not allow an assessment of their relative importance or an evaluation of possible interactions among diversity levels. In order to disentangle the relative roles of both levels of diversity, experiments are warranted that manipulate species diversity and genetic diversity in factorial combination (Vellend and Geber 2005). Aquatic macrophyte stands that are composed of a few species, all with facultative clonal reproduction (Engelhardt and Ritchie 2001), seem ideal to design such experiments. Another target community for addressing such questions would be fouling communities whose members, such as bryozoans, tunicates, or cnidarians, often also exhibit clonal growth.

OTHER MARINE SYSTEMS

While the available studies addressing the role of genetic diversity encompass only a few species in an even smaller number of community types, we can predict when analogous effects should emerge and matter. The importance of genetic diversity should increase as the genetic differentiation between genotypes grows. Findings of strong genotype differences in the salt marsh plant *Spartina alterniflora* (Proffitt 2003) make it highly plausible that similar aggregate diversity responses would occur if genotypic diversity had been a treatment factor.

Genetic differences among pelagic phytoplankton strains that are correlated with important functional variation in light and nutrient tolerances (Dufresne et al. 2003; Rocap et al. 2003) suggest that intraspecific diversity may be linked with increased productivity and nutrient utilization (Duffy and Stachowicz in press). Higher resource utilization would presumably translate into significant positive complementarity effects at the population level and into positive biodiversity-productivity relationships.

SPECIES INTERACTIONS AND COEVOLUTION

Under which conditions do effects of macrophyte genetic diversity transfer up to higher trophic levels? In terrestrial plants, strong effects of the host plant genotype on the composition of the arthropod community have recently been identified (Johnson et al. 2006; Wimp et al. 2005). Macrophyte genetic diversity could influence higher trophic levels directly through its effects on plant structure or productivity, or indirectly by affecting the diversity or abundance of epiphytic algae (Honkanen and Jormalainen 2005) that is often the preferred resource of associated invertebrates. Current evidence suggests that in seagrasses, genetic diversity can positively influence closely associated invertebrates (Hughes and Stachowicz 2004; Reusch et al. 2005), but how this translates to the next trophic levels, such as more mobile invertebrate and fish species, is unclear. Because the diversity of grazing species can have major effects on seagrass ecosystem functioning (Duffy et al. 2003; Duffy in press), interesting feedback loops between genetic diversity and the species diversity of higher trophic levels can be postulated (e.g., Johnson et al. 2006) with as yet unknown consequences for the functioning of the entire system.

Although this perspective focuses on immediate ecological effects of diversity, trait and associated fitness differences among genotypes will translate into contemporary (i.e., rapid) evolution. Species interactions are not static but may be molded by rapid coevolutionary processes (Stockwell et al. 2003). Good candidates for rapid coevolution include host-epiphyte and host-pathogen interactions. Epiphytic algae can have strong effects on seagrasses (Hughes et al. 2004) and other macrophytes, yet it is unknown how the species or genetic diversity of epiphytes interacts with the genetic diversity of the host species. Disease can also be an important force in estuarine macrophytes (wasting disease in eelgrass). Host-pathogen interactions may become particularly important in light of emerging marine disease (Harvell et al. 2002). Both the genetic diversity of pathogen virulence genes and of the defence genes of hosts will interact. Local population persistence will depend upon sufficient

genetic diversity of resistance genes of the host plant population.

CONCLUSIONS

Recent experiments in coastal plant communities generalize the relationship between diversity and ecosystem function. Effects and underlying mechanisms of genotypic and species diversity on ecosystem functioning are analogous. Further development of molecular tools will soon allow an integrative experimental approach to address consequences of biological diversity at the genotypic, genetic (sensu strictu), and species level (Montalvo et al. 1997). Seagrass beds are threatened by a number of anthropogenic perturbations (Short and Wyllie-Escheverria 1996), and research has demonstrated that restoration efforts of seagrasses may lead to beds with reduced genetic diversity compared to natural sites (Williams 2001). Recent findings provide an empirical basis for explicitly considering the maintenance of genetic-genotypic diversity when protecting or restoring coastal marshes or seagrass beds.

ACKNOWLEDGMENTS

LITERATURE CITED

ANTONOVICS, J. 1976. The input from population genetics: The new ecological genetics. *Systematic Botany* 1:233–245.

ASHLEY, M. V. AND B. D. DOW. 1994. The use of microsatellite analysis in population biology: Background, methods and potential applications, p. 186–201. *In* B. Schierwater, B. Streit, G. P. Wagner, and R. DeSalle (eds.), Molecular Ecology and Evolution, Approaches and Application. Birkhäuser, Basel, Switzerland.

BALLOUX, F., W. AMOS, AND T. COULSON. 2004. Does heterozygosity estimate inbreeding in real populations? *Molecular Ecology* 13: 3021–3031.

BENSCH, S. AND M. AKESSON. 2005. Ten years of AFLP in ecology and evolution: Why so few animals? *Molecular Ecology* 14: 2899–2914.

BOCKELMANN, A. C., T. B. H. REUSCH, R. BIJLSMA, AND J. P. BAKKER. 2003. Habitat differentiation vs. isolation-by-distance: The genetic population structure of *Elymus athericus* in European salt marshes. *Molecular Ecology* 12:505–515.

BOOTH, R. E. AND J. P. GRIME. 2003. Effects of genetic impoverishment on plant community diversity. *Journal of Ecology* 91: 721–730.

COSTANZA, R., R. D'ARGE, R. DE GROOT, S. FARBER, M. GRASSO, B. HANNON, K. LIMBURG, S. NAEEM, R. V. O'NEILL, J. PARUELO, R. G. RASKIN, P. SUTTON, AND M. VAN DEN BELT. 1997. The value of the world's ecosystem services and natural capital. *Nature* 387: 253–260.

COYER, J. A., A. F. PETERS, W. T. STAM, AND J. L. OLSEN. 2003. Post-ice age recolonization and differentiation of *Fucus serratus* L.

(Phaeophyceae; Fucaceae) populations in Northern Europe. *Molecular Ecology* 12:1817–1829.

DAVID, P. 1998. Heterozygosity-fitness correlations: New perspectives on old problems. *Heredity* 80:531–537.

DUFFY, J. E. in press. Biodiversity and the functioning of seagrass ecosystems. *Marine Ecology Progress Series.*

DUFFY, J. E., J. P. RICHARDSON, AND E. A. CANUEL. 2003. Grazer diversity and ecosystem functioning in seagrass beds. *Ecology Letters* 6:637–645.

DUFFY, J. E. AND J. J. STACHOWICZ. In press. Why biodiversity is important to oceanography. *Marine Ecology Progress Series.*

DUFRESNE, A., M. SALANOUBAT, F. PARTENSKY, F. ARTIGUENAVE, I. AXMANN, V. BARBE, D. S. M. Y. GALPERIN, E. V. KOONIN, F. LE GALL, K. S. MAKAROVA, M. OSTROWSKI, S. OZTAS, C. ROBERT, I. B. ROGOZIN, D. J. SCANLAN, N. T. DE MARSAC, J. WEISSENBACH, P. WINCKER, Y. WOLF, AND W. R. HESS. 2003. Genome sequence of the cyanobacterium *Prochlorococcus marinus* SS120, a nearly minimal oxyphototrophic genome. *Proceedings of the National Academy of Sciences USA* 100:10020–10025.

EMMERSON, M. C., M. SOLAN, C. EMES, D. M. PATERSON, AND D. RAFFAELLI. 2001. Consistent patterns and the idiosyncratic effects of biodiversity in marine ecosystems. *Nature* 411:73–77.

ENGELHARDT, K. A. M. AND M. E. RITCHIE. 2001. Effects of macrophyte species richness on wetland ecosystem functioning and services. *Nature* 411:687–689.

FOX, J. W. 2005. Interpreting the 'selection effect' of biodiversity on ecosystem function. *Ecology Letters* 8:846–856.

HÄMMERLI, A. AND T. B. H. REUSCH. 2003. Inbreeding depression influences genet size distribution in a marine angiosperm. *Molecular Ecology* 12:619–629.

HARVELL, C. D., C. E. MITCHELL, J. R. WARD, S. ALTIZER, A. P. DOBSON, R. S. OSTFELD, AND M. D. SAMUEL. 2002. Climate warming and disease risks for terrestrial and marine biota. *Science* 296:2158–2162.

HEMMINGA, M. A. AND C. M. DUARTE. 2000. Seagrass Ecology. Cambridge University Press, Cambridge, Massachusetts.

HILBORN, R., T. P. QUINN, D. E. SCHINDLER, AND D. E. ROGERS. 2003. Biocomplexity and fisheries sustainability. *Proceedings of the National Academy of Sciences USA* 100:6564–6568.

HONKANEN, T. AND V. JORMALAINEN. 2005. Genotypic variation in tolerance and resistance to fouling in the brown alga *Fucus vesiculosus. Oecologia* 144:196–205.

HUGES, A. R. K. J. BANDO, L. F. RODRIGUEZ, AND S. L. WILLIAMS. 2004. Relative effects of grazers and nutrients on seagrasses: A meta-analysis approach. *Marine Ecology Progress Series* 282:87–99.

HUGHES, A. R. AND J. J. STACHOWICZ. 2004. Genetic diversity enhances the resistance of a seagrass ecosystem to disturbance. *Proceedings of the National Academy of Sciences USA* 101:8998–9002.

JOHNSON, M. T. J., M. J. LAJEUNESSE, AND A. A. AGRAWAL. 2006. Additive and interactive effects of plant genotypic diversity on arthropod communities and plant fitness. *Ecology Letters* 9:24–34.

JONES, C. G., J. H. LAWTON, AND M. CHACHAK. 1994. Organisms as ecosystem engineers. *Oikos* 69:373–386.

LI, Y.-C., A. B. KOROL, T. FAHIMA, AND E. NEVO. 2004. Microsatellites within genes: Structure, function, and evolution. *Molecular Biology and Evolution* 21:991–1007.

LOREAU, M. AND A. HECTOR. 2001. Partitioning selection and complementarity in biodiversity experiments. *Nature* 412:72–76.

LOREAU, M., S. NAEEM, and P. INCHAUSTI (EDS.). 2002. Biodiversity and Ecosystem Functioning: Synthesis and Perspective. Oxford University Press, Oxford, U.K

LOREAU, M., S. NAEEM, P. INCHAUSTI, J. BENGTSSON, J. P. GRIME, A. HECTOR, D. U. HOOPER, M. A. HUSTON, D. RAFFAELLI, B. SCHMID, D. TILMAN, AND D. A. WARDLE. 2001. Biodiversity and ecosystem functioning: Current knowledge and future challenges. *Science* 294:804–808.

LUIKART, G., P. R. ENGLAND, S. JORDAN, AND P. TABERLET. 2003. The power and promise of population genomics: From genotyping to genome typing. *Nature Reviews in Genetics* 4:981–994.

Lynch, M. 1996. A quantitative-genetics perspective on conservation issues, p. 471–501. *In* J. C. Avise (ed.), Conservation Genetics. Chapman and Hall, New York.

Milligan, B. G., J. Leebens-Mack, and A. E. Strand. 1994. Conservation genetics: Beyond the maintenance of marker diversity. *Molecular Ecology* 3:423–435.

Montalvo, A. M., S. L. Williams, K. J. Rice, S. L. Buchmann, C. Cory, S. N. Handel, G. P. Nabhan, R. Primack, and R. H. Robichaux. 1997. Restoration biology: A population biology perspective. *Restoration Ecology* 5:277–290.

Morin, P. A., G. Luikart, R. K. Wayne, the SNP group. 2004. SNPs in ecology, evolution and conservation. *Trends in Ecology and Evolution* 19:208–216.

Olsen, J. L., W. T. Stam, J. A. Coyer, T. B. H. Reusch, M. Billingham, C. Boström, E. Calvert, H. Christie, S. Granger, R. La Lumiere, N. Milchakova, M.-P. Oudot Le-Seq., G. Procaccini, B. Sanjabi, E. Serrao, J. Veldsink, S. Widdicombe, and S. Wyllie-Echeverria. 2004. Population differentiation and post-ice age recolonization of the North Atlantic by the seagrass *Zostera marina* L. *Molecular Ecology* 13:1923–1941.

Paine, R. T. 2002. Trophic control of production in a rocky intertidal community. *Science* 296:736–739.

Pimm, S. L. 1984. The complexity and stability of ecosystems. *Nature* 307:321–326.

Procaccini, G., L. Orsini, M. V. Ruggiero, and M. Scardi. 2001. Spatial patterns of genetic diversity in *Posidonia oceanica*, an endemic Mediterranean seagrass. *Molecular Ecology* 10:1413–1421.

Procaccini, G. and L. Piazzi. 2001. Genetic polymorphism and transplantation success in the Mediterranean seagrass *Posidonia oceanica*. *Restoration Ecology* 9:332–338.

Proffitt, C. E. 2003. Genotype and elevation influence *Spartina alterniflora* clonization and growth in a created salt marsh. *Ecological Applications* 13:180–192.

Reusch, T. B. H., A. Ehlers, A. Hämmerli, and B. Worm. 2005. Ecosystem recovery after climatic extremes enhanced by genotypic diversity. *Proceedings of the National Academy of Sciences USA* 102:2826–2831.

Reusch, T. B. H., W. T. Stam, and J. L. Olsen. 2000. A microsatellite-based estimation of clonal diversity and population subdivision in *Zostera marina*, a marine flowering plant. *Molecular Ecology* 9:127–140.

Rocap, G., F. W. Larimer, J. Lamerdin, S. Malfatti, P. Chain, N. A. Ahlgren, A. Arellano, M. Coleman, L. Hauser, W. R. Hess, Z. I. Johnson, M. Land, D. Lindell, A. F. Post, W. Regala, M. Shah, S. L. Shaw, C. Steglich, M. B. Sullivan, C. S. Ting, A. Tolonen, E. A. Webb, E. R. Zinser, and S. W. Chisholm. 2003. Genome divergence in two *Prochlorococcus* ecotypes reflects oceanic niche differentiation. *Nature* 424:1042–1047.

Schär, C., P. L. Vidale, D. Lüthi, C. Frei, C. Häberli, M. A. Liniger, and C. Appenzeller. 2004. The role of increasing temperature variability in European summer heat waves. *Nature* 427:332–335.

Short, F. T. and S. Wyllie-Escheverria. 1996. Natural and human-induced disturbance of seagrasses. *Environmental Conservation* 25:17–27.

Stachowicz, J. J., H. Fried, R. W. Osman, and R. B. Whitlach. 2002. Biodiversity, invasion resistance, and marine ecosystem function: Reconciling pattern and process. *Ecology* 83:2575–2590.

Stockwell, C. A., A. P. Hendry, and M. T. Kinnison. 2003. Contemporary evolution meets conservation biology. *Trends in Ecology and Evolution* 18:94–101.

Travis, S. E. and M. W. Hester. 2005. A space-for-time substitution reveals the long-term decline in genotypic diversity of a widespread salt marsh plant, *Spartina alterniflora*, over a span of 1500 years. *Journal of Ecology* 93:417–430.

van Tienderen, P. H., A. A. de Haan, C. G. van der Linden, and B. Vosman. 2002. Biodiversity assessment using markers for ecologically important traits. *Trends in Ecology and Evolution* 17:577–583.

Vellend, M. and M. A. Geber. 2005. Connections between species diversity and genetic diversity. *Ecology Letters* 8:767–781.

Welsh, J., C. Petersen, and M. McClelland. 1991. Polymorphism generated by arbitrarily primed PCR in the mouse: Application to strain identification and genetic mapping. *Nucleic Acid Research* 19:303–306.

Williams, S. L. 2001. Reduced genetic diversity in eelgrass transplantations affects both population growth and individual fitness. *Ecological Applications* 11:1472–1488.

Wimp, G., G. D. Martinsen, K. D. Floate, R. K. Bangert, and T. G. Whitham. 2005. Plant genetic determinants of arthropod community structure and diversity. *Evolution* 59:61–69.

Woodhead, M., J. Russell, J. Squirrell, P. M. Hollingsworth, K. MacKenzie, M. Gibby, and W. Powell. 2005. Comparative analysis of population genetic structure in *Athyrium distentifolium* (Pteridophyta) using AFLPs and SSRs from anonymous and transcribed gene regions. *Molecular Ecology* 14:1681–1695.

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