



## THEME SECTION

# Bridging the gap between aquatic and terrestrial ecology

*Idea and coordination:* Konstantinos I. Stergiou, Howard I. Browman

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## Introduction

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Although terrestrial and aquatic ecosystems differ in various respects (e.g. Carr et al. 2003), they are also strongly linked (e.g. Polis & Hurd 1995, Gende et al. 2002, Brashares et al. 2004, Knight et al. 2005, Orr et al. 2005). Unfortunately, ecologists working on these 2 eco-domains are, at best, only weakly linked. Steele (1995, p. 16) states: 'I have emphasized the separation between marine and terrestrial ecological studies because there are major differences in concepts, in organization, and in funding'. Analyses referring to the 'conservation' part of ecology (Irish & Norse 1996,

Kochin & Levin 2003, Ormerod 2003) show that Steele's remark is supported by quantitative evidence. Not only this, but 'Unfortunately, ecologists who specialize in certain types of ecosystem tend to favor particular hypotheses and observations, and discount hypotheses and observations noted in other ecosystems.' (Chase 2000, p. 412). Such barriers to communication, whether real or perceived, undoubtedly slow down progress in ecology as a discipline, and have profound implications for its advancement and effectiveness.

Comparisons across eco-domains allow us to (1) identify the need for developing new theories and/or models for particular ecotypes (e.g. marine food webs: Link 2002; epidemiology: McCallum et al. 2004); (2) identify widely applicable ecological processes and develop nomothetic approaches to address critical ecological issues (see also Steele 1991, 1995, Chase 2000); and (3) design conservation plans and policies that

\*Contributions are in alphabetical order (by first author)

\*\*The views expressed herein are my own and do not necessarily reflect the official position of The Institute of Marine Research

appropriately consider eco-domain-specific differences (e.g. Carr et al. 2003). Therefore, a cross-eco-domain approach would unquestionably contribute to the maturation of ecology as a discipline.

In order to bring these issues into focus, we asked contributors to this Theme Section to discuss 'communication barriers' amongst ecologists. The contributions generally indicate that there is in fact a gap between terrestrial and aquatic ecologists: they are educated and trained differently, often using different approaches and tools, and addressing different questions; they read, publish in, and cite different journals; they assemble in different scholarly societies; and they are funded from different sources. Yet, whenever they meet, the outcome is mutually rewarding and to the benefit of the discipline. Steele (1995, p. 16) maintains that 'The longstanding nature of this dichotomy implies that convergence of these sub-disciplines will not be easy and cannot be rapid.' We hope that this Theme Section will be viewed as a small step in the right direction.

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## Communication between terrestrial and marine ecologists: loud, sometimes abrasive, but healthy and occasionally useful

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In this brief essay I will touch upon only a few of the topics suggested by the editors of this section, those where I feel that I have some actual knowledge. In doing this I would like to make a point: there are gaps between terrestrial, marine and freshwater ecology. These gaps have bridges, but these bridges are fettered with obstacles. There are interesting trends in ecology, which would seem, paradoxically, to both increase the fragmentation among sub-disciplines and create at the same time enormous opportunities for differently trained scientists to work together. My views of this situation are clearly colored by being both a citizen of the USA and someone who has done research in both oceanography and limnology.

**Communication is loud and healthy at the global scale.** With some pressing problems occurring at the global scale and in globally distributed reservoirs like the ocean and the atmosphere, I think we are seeing a great deal of very positive communication between marine and terrestrial ecologists. This communication has not always been harmonious or even polite, but communicate we certainly have. During the 1980s, for example, there was a huge debate about whether or not the terrestrial biosphere was a source or sink of atmospheric CO<sub>2</sub> in addition to the obvious combustion of fossil fuel. Good satellite images were newly available to terrestrial ecologists and noted scientists such as Dr. George Woodwell (Woods Hole Research Center) could plainly see that vast areas of land were being converted from forest to agriculture. Intensive studies at these sites showed that without doubt, and for a variety of reasons in addition to removing the trees, there was much less organic carbon on the land plots than had been there prior to massive deforestation (Houghton & Woodwell 1989). The global atmospheric and oceanic budgets of CO<sub>2</sub> suggested, conversely, that terrestrial

forests had to be a net sink of CO<sub>2</sub>. This global balance was based on the measured rise of CO<sub>2</sub> in the atmosphere using C. D. Keeling's remarkable record of atmospheric CO<sub>2</sub> increases (see Keeling 1998), on estimates of fossil fuel combustion, and calculations of how much of the CO<sub>2</sub> emitted to the atmosphere could be transferred into the ocean. Oceanographers were fairly confident about the magnitude of the oceanic CO<sub>2</sub> sink. Noted scientists like Wally Broecker were able to constrain the size of the oceanic sink using a variety of tools such as the penetration of bomb <sup>14</sup>C in the ocean and modeling <sup>13</sup>C in atmospheric CO<sub>2</sub>. The fossil fuel combusted minus the increase of CO<sub>2</sub> in the atmosphere, minus the amount estimated to enter the ocean was still a fairly large positive number. If it was not in the atmosphere (measured) or entering the oceans (a good estimate, or so said the oceanographers) the residual CO<sub>2</sub> had to be stored somewhere on land, probably in forests. The oceanographer's 'missing terrestrial C sink' flew in the face of reason to many terrestrial ecologists watching global-scale deforestation. I once heard Dr. Woodwell and Dr. Broecker debate this at Woods Hole. Faces were red with anger, names like 'leaf counter' and 'geochemical fool' were thrown about loudly. For a young post-doc it was certainly a lot of fun watching famous oceanographers and terrestrial ecologists 'communicate.' The field of global carbon cycling, however, was enormously advanced by these acrimonious interactions. The ocean takes up somewhat more CO<sub>2</sub> than Broecker originally estimated, and more subtle reforestation in the Northern Hemisphere, at least in theory, compensates for the more visible deforestation in the tropics. Terrestrial ecologists have accepted the idea that there must be a net sink for CO<sub>2</sub> somewhere on the continents and have launched extensive scientific measurement programs to find it. Terrestrial ecologists now also think more about a hemispherical reorganization of carbon biomass (Schimel et al. 1990). A picture of the controversy as it was in the mid 1980s is nicely explained in Hobbie et al. (1985). The point is that oceanographers and terrestrial ecologists addressed the same question, albeit with different tools, biases, and notions about which data and which approaches were good and bad. They communicated.

**The Ecosystem concept is growing in the oceanographic community.** One of the more useful concepts in ecology during the past 50 yr has been that of the ecosystem. An ecosystem is defined as a '... spatially explicit unit of the Earth that includes all of the organisms, along with all components of the abiotic environment within its boundaries.' (Likens 1992). The words 'spatially explicit' mean that an ecosystem has boundaries. Even if the boundaries are arbitrary their existence is extremely useful. Looking at the world as a series of ecosystems allows one to construct meaning-

ful mass balances. For a biogeochemist, these mass balances provide the basic constraints to understand processes within ecosystems. For a long time the ecosystem approach was widely adopted in terrestrial ecology, largely using the watershed as the ecosystem unit, and in limnology, using the lake or stream system. More recently, we are seeing oceanographers speak of marine ecosystems and at least use this common language when talking about mass balances. This use of the word 'ecosystem' in conjunction with oceanography is on the increase. Putting 'ocean' and 'ecosystem' into the search engine Web of Science (WOS) turned up 1391 references back to 1975 (as far back as WOS goes). Of these, 86% have occurred in the last decade (since 1995) and 72% have been since 1998 (see e.g. Karl 1999, Sherman et al. 2003). This trend is very encouraging, as it will likely enhance communication among scientists working on different ecosystems (terrestrial, marine, freshwater). Even more encouraging is that we are seeing the use of the word 'ecosystem' in a wide array of very different journals (e.g. *Global Biogeochemical Cycles*, *Ecosystems*, *Deep Sea Research*, *Journal of Oceanography*, and of course *Marine Ecology Progress Series*).

**Few barriers at the smallest scales.** As someone who works in microbial ecology, mostly in freshwaters, I find that oceanographers and limnologists see almost no barriers at all between them. For as long as I have been involved in this endeavor, limnologists and oceanographers have attended the same meetings, published in the same journals, compared rates across marine and freshwater systems, and shared and extended techniques and insights. In the mid 1980s there was an acrimonious debate about how to measure the secondary production of bacteria. The debaters could perhaps have been more polite with each other, but my point is that limnologists and oceanographers were together in this up to their collective eyeballs. Older journals like *Limnology and Oceanography* or *Marine and Freshwater Research*, as well as newer journals like *Aquatic Microbial Ecology*, have both benefited by this community of mixed salinity researchers and have helped the field along. In the USA it is very common in the microbial sector for someone to get part of his or her training in freshwaters (say the PhD) and then do post-doctoral work in the ocean. There is a much larger communication gap, I fear, between the aquatic microbial ecologists and those working on soil. With regard to the genetic sequencing techniques, we are all on the same page. With regard to rate measurements, a very big part of aquatic microbial ecology, we are worlds apart. It is, of course, more difficult to measure a rate of bacterial production in a heterogeneous environment like soil than it is in the plankton. But it does seem that the soil

microbiologists and those working on aquatic habitats are not communicating well at all. The folks who work on freshwater and marine sediments have many of the same problems as those working in forest or agricultural soils, yet they seem to be more in contact with pelagic microbial ecologists.

**Scientific journals and funding agencies actually cause some separation.** At the global scale, for the reasons described above, there are a few key journals that help the integration of oceanography with terrestrial ecology because they are focused on global element cycles. Similarly, at the microbial scale there are at least a few journals which cover the entire spectrum of terrestrial and aquatic work (for example, *Microbial Ecology* or *Applied and Environmental Microbiology*). There are very few journals that publish both marine and terrestrial ecology at intermediate spatial scales within their covers. The journals of the Ecological Society of America (ESA) do this to a small degree in *Ecology*, *Ecological Applications* and *Ecological Monographs*, but the quantity of marine ecology is quite low in these. *Biogeochemistry* and *Ecosystems* do this to a much larger degree as, hopefully, will the new European *Biogeosciences* journal. Most scientific societies draw or inadvertently create a somewhat inhibitory boundary at the land–water interface, particularly at the salty end. Very little oceanography is presented at the ESA meetings, for example, and very little terrestrial ecology is presented at ASLO (American Society of Limnology and Oceanography) meetings. This unintentional boundary is striking, because there is a great deal of interest in the connections between land and water in terms of nutrient inputs from land to the sea, the effect of terrestrial carbon on aquatic systems, and so on. The funding system, at least in the USA, also has a boundary to some extent where land meets the sea. At the National Science Foundation (NSF), for example, the Ecosystem Studies Program funds a lot of wonderful work in terrestrial and freshwater ecosystems, but very little in salt water. The Ecosystems Studies Program is part of a group of programs with the Biological Directorate. If salt water is involved in a major way, then it is funded by a different part of NSF, the Oceanography Program. This program is located in a different Directorate as well, the Geosciences. The boundaries have very recently been growing less severe. There are now several Long Term Ecological Research sites funded through NSF that involve coastal systems ([www.lternet.edu/](http://www.lternet.edu/)). Nevertheless, all the way from the review of proposals to the presentation and publication of results, there are still some factors which tend to keep terrestrial and marine ecology separated.

There is a strong trend in the USA to support interdisciplinary science. At least scientists often push the funding structure to improve the climate for more

interdisciplinary approaches to science. This support comes in many forms, including programs to train graduate students across disciplines, special funding opportunities that reach across disciplines, and the occasional conference that directly attempts to bridge a perceived gap between disciplines. The terrestrial ecologists I interact with seem to be emphasizing cooperation with the social sciences. There are a large number of terrestrial ecology programs which are cross-training students in social science, economics, environmental policy and related endeavors. This marriage is not a random idea. It is widely thought that the solutions to many environmental problems most likely lie at the intersection of environmental science and some aspect of social science. I have never encountered a program which attempts to cross-train marine and terrestrial ecologists. Certainly the societal pay-off for this could be substantial, because a large number of problems in the coastal environment originate on land. The scientific pay-off could be equally large, and now is probably a very good time to launch such a program.

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## Comparing aquatic and terrestrial variability: at what scale do ecologists communicate?

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**Introduction.** Throughout the last 2 decades, the concept of scale has proven very useful in all fields of environmental science, including ecology. But is this more true for terrestrial than aquatic ecology?

In a review of scale in ecology by the terrestrial ecologist Simon Levin (1992), only 13% of the papers cited were on aquatic themes as opposed to terrestrial or general ecology. In a later review by David Schneider (2001), a marine ecologist, the proportion of aquatic references was still only a quarter. In a more recent review on the closely related theme of fractals in ecology, in which I participated (Halley et al. 2004), we only found 3 relevant papers on aquatic themes out of >100 papers cited. Overall, this does suggest either that the idea of scale matters less to aquatic specialists than to their terrestrial counterparts, or that there is a communication (or reading) gap.

The term 'scale' loosely signifies the characteristic magnitude of a phenomenon in space or time. For example, ice ages are associated with changes in glaciation affecting areas several 1000 km across that typically occur over periods of between 10 000 and 50 000 years, so ice ages can be associated with a spatial scale of '1000s of km' and a temporal scale in '10 000s of years'. In this essay, I will discuss the development of the concept of scale, especially the temporal scale of ecological variability. I will be paying special attention to the way in which aquatic and terrestrial ecology have influenced each other. This way, it is possible to see (1) what kind of communication barrier, if any, separates aquatic from terrestrial ecologists, (2) whether there is some sort of paradigm difference between the 2 fields and, (3) how we can gain from large-scale comparisons between the structure and function of aquatic and terrestrial ecosystems.

**Steele's conjectures.** In a seminal paper, John Steele (1985) pointed out that the marine environment is fundamentally different from the terrestrial one. Not only is this true of the amount of environmental variability, but also of its rhythms. While on land the variance of significant abiotic factors such as temperature stays more or less constant (yearly variability does not differ systematically from monthly variability and so on), this is not so in the marine environment. Instead, in the ocean, the amount of variance depends on how long you observe it, increasing continuously from hourly scales upwards. The typical variability of sea surface temperature (SST) over a year, for example, will be much larger than the variability observed over a month. It is also true that if you measure the SST on the first day of each month, the variance of this set will be greater than that of a set of 12 consecutive days. This phenomenon is called 'variance growth' and this growth depends not on the number of observations taken, but on the temporal scale that they span. This assertion has been confirmed in 2 recent papers (Cyr & Cyr 2003, Vasseur & Yodzis 2004) that carefully examined a wide range of environmental variables, including air and water temperature in or around

lakes, rivers and seas, as well as extremes of temperature, ice cover and precipitation. Although there are some provisos (e.g. blurring of distinction in coastal regions; less-than-expected low frequency variation; inapplicability to extreme-value data), this work broadly confirms that the marine environment is indeed more 'reddened' (Fig. 1) than the terrestrial one.

Such a profound difference between terrestrial and marine environments ought to leave a signature on population dynamics:

One should expect the internal dynamics and structures of marine and terrestrial systems, particularly at the higher trophic levels, to differ in significant ways in response to the temporal character of each physical environment. This does not mean that comparisons cannot and should not be made (Steele 1985, p. 358).

Steele's (1985) paper introduced into ecological discussion the idea of a 'reddened environment'. A reddened environment, such as the ocean, is one in which slower processes, such as large oceanic gyres, account for more environmental variability than relatively rapid processes (e.g. small eddies). This redness, which is associated with variance growth, is due to long-term temporal autocorrelations of temperature.

A subsequent paper noted that terrestrial ecologists tend to 'emphasize the importance of density dependence through detailed consideration of prey-predator or competitive-community interactions' (Steele & Henderson 1994, p. 5) with much less scrutiny on 'environmental perturbations', while 'the marine view would be that relatively large-scale processes, such as El Niño, are the significant factors in population variability (apart from human harvesting)' (p. 5). Steele & Henderson suggested that the fundamental reason for these different approaches of marine and terrestrial ecologists was the 'overlap in the space- and time-scales of ocean physics and biology, compared with the separation between these scales in most atmospheric and terrestrial systems' (p. 5). They predicted that as ecologists of both fields started to look at wider ranges of time scales, they would be forced to use a more integrated approach: marine ecologists would turn more to population dynamics and terrestrial ecologists would focus more on the environment (see Stenseth et al. 2005, in this Theme Section). The powerful device used in Steele & Henderson's paper was to interpret environmental variability in terms of temporal scale. By portraying the spectrum of environmental variability on a scale-by-scale basis, it was possible to see how different processes (e.g. El Niño, ice ages) kicked in on different time scales. The intimidating 'environment' term of ecological models could be understood as a collection of simpler processes, each with its own temporal sphere of influence. This jungle of uncharted stochasticity now had a type of roadmap. Steele &

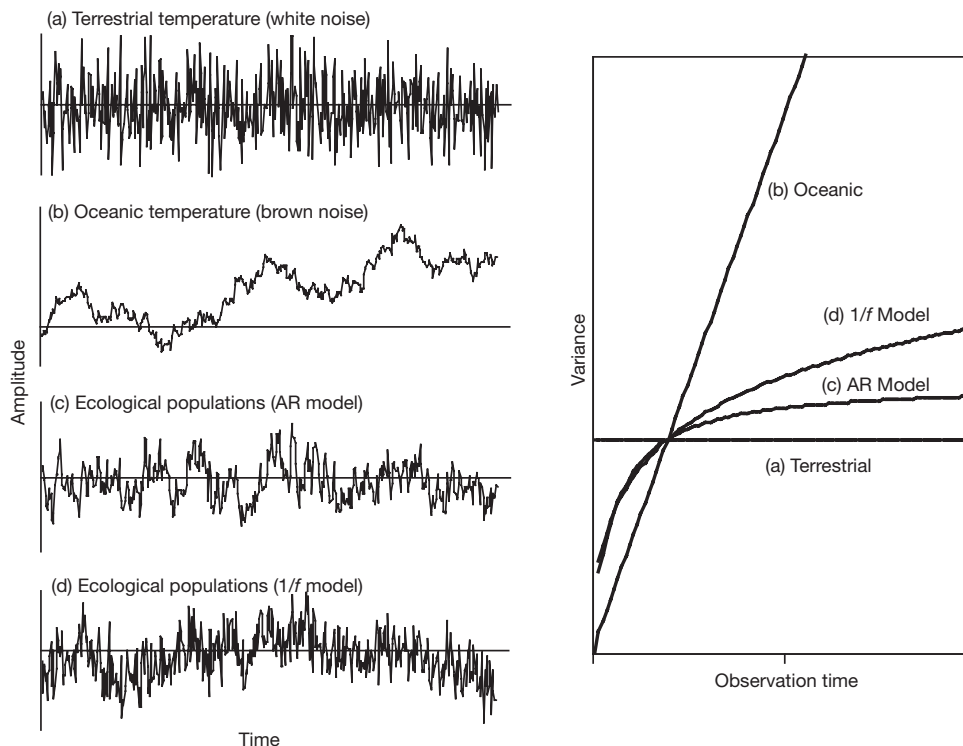


Fig. 1. Models of variability. (a) White noise is a reasonable model of terrestrial temperature variation. (b) Brown noise (also called  $1/f^2$  noise) is more suitable for oceanic temperatures. Ecological populations have been modelled both by (c) autoregressive (AR) processes and (d) pink  $1/f$  noise; Models (c) and (d) are difficult to distinguish in the case of short series. For the reddened models, (b) to (d), variance grows with observation time. The panel on the right shows the corresponding patterns of the expected variance increase. For ecological populations the rate of variance increase tends to slow down

Henderson (1994) argued that there was a fundamental difference in paradigm between aquatic (especially marine) ecologists and their terrestrial counterparts, and that this led to different approaches to explaining complexity. The device that they used to explain this contrast, the notion of scale dependence, was taken up with enthusiasm by terrestrial ecologists.

**An idea born in the sea.** It is not surprising that marine ecologists were the first to appreciate the importance of the concept of scale. Oceanic processes vary over a vast range of scales: in time from seconds to 100s of years and in space from  $\mu\text{m}$  to 1000s of km. Yet even to an oceanographer, one part of the ocean's surface looks remarkably like all the rest. So why then are there so many species in the plankton, for example, when the sea apparently has no structure? On land, ecologists could focus on how different communities arise as a result of different habitats (e.g. forest, grassland) with clear boundaries. Without the panacea of real or imagined habitat boundaries, oceanographers and aquatic ecologists were bound to feel the need for an alternative conceptual framework, one that was not based on physical boundaries. A pictorial scheme developed by Stommel (1963) provided such a framework (Table 1), the Stommel diagram. It was based

on the concept of spatial and temporal scale. In the Stommel diagram, the 'distribution ... [is] plotted as a function of logarithmic scales of space and time. The vertical axis was used to represent the amount of fluctuation' (Haury et al. 1978, p. 278). The scheme was introduced into aquatic ecology in a volume edited by Steele (1978). However, it was not until the late 1980s that the idea of scale really took off in ecology. Schneider identifies this decade as a period of 'paradigm shift' towards the concept of scale in ecology (Schneider 2001, p. 546).

The growing appreciation of scale in ecology was part of a wider revolution. Throughout the 1980s, in many fields of science there was an increasing preoccupation with issues of scale. The pioneering work (and vigorous campaigning) of Benoit Mandelbrot (1977) ensured that this issue of scale would be taken seriously. Mandelbrot's work brought a new way of looking at scale and a mathematical formalism (power laws, scale-symmetry, self-affinity, and fractality) to go with it. Of course, power laws had been around for many years. For example, in ecology Taylor's power law and the various allometric relations have been used widely. However, the unifying conceptual framework provided by Mandelbrot and others gave these laws greater significance. Also, many phenomena previ-

Table 1. Some milestones in the study of temporal scale in ecology—the list is not exhaustive. A (in 3rd column): at least 1 aquatic ecologist was involved; A (in 4th column): published in an aquatic ecology journal or book

| Year      | Author  | Team | Source | Concept(s)  |
|-----------|---|------|--------|---|
| 1963      | Stommel                                       | A    |        | Diagrammatic representation of scale  |
| 1977      | Mandelbrot                                    |      |        | Mathematical theory of scale: fractals  |
| 1978      | Steel, Haury et al.                           | A    | A      | Ecological application of Stommel's diagram   |
| 1985      | Steele  | A    |        | Differences in redness between marine and terrestrial systems                                     |
| 1988–1989 | Pimm & Redfearn;<br>and others                |      |        | Redness as a cause of variance growth for populations;<br>subsequent debate about this            |
| 1992      | Baumgartner et al.                            | A    | A      | Millennium-scale reconstructed time series  |
| 1992      | Levin   |      |        | Review of pattern and scale in ecology  |
| 1994      | Steele & Henderson                            | A    |        | Coupling of physical and biological scales  |
| 1995      | Cohen   |      |        | Chaotic models imply blue, not red, spectra   |
| 1996      | Halley  |      |        | 1/f-noise model of ecological variability   |
| 1996–1997 | Ripa & Lundberg;<br>Johst & Wissell           |      |        | Theoretical exploration of the implications of reddening for<br>extinction forecasts              |
| 1997      | Cyr   | A    |        | Observation of slower variance increase for freshwater<br>(mostly planktonic) species             |
| 1998      | Miramontes & Rohani                           |      |        | Demonstration that population redness may be intrinsic,<br>not environmentally forced             |
| 1998      | Cohen et al.<br>(see also Petchy 2000)        | A    |        | Aquatic microcosms using 1/f-noise forcing  |
| 1998      | Stergiou                                      | A    | A      | Report of variance growth of fish landings  |
| 1999–2000 | Heino et al.; Morales;<br>Cuddington & Yodzis |      |        | Analyses of subtle problems arising in ecological models driven by<br>coloured noise              |
| 2001      | Schneider                                     | A    |        | Review of scale in ecology  |
| 2003      | Vasseur & Yodzis;<br>Cyr & Cyr                | A    |        | Nuanced confirmation of differences in variability between marine<br>and terrestrial environments |
| 2005      | Halley & Stergiou                             | A    | A      | Comparison between marine and terrestrial populations   |

ously described by other means were now cast in terms of power laws. For example, a seemingly obscure topic of electrical engineering, the  $1/f$  family of noises, would become relevant to a wider audience of environmental scientists including ecologists (Halley 1996). Steele (1985) noted that the spectrum of marine environmental variability was  $1/f^2$ , in contrast to the flat ( $1/f^0$ ) spectrum of terrestrial environmental variability. Steele was thus casting the issue of reddened environments as a tale of 2 power laws, in terms of scaling. This was one of the ideas taken up later by terrestrial ecologists.

**Timescales and redness in terrestrial ecology.** An idea that appealed to terrestrial ecologists was that variability changes according to the timescale on which it is observed. An important paper by Pimm & Redfearn (1988) applied it to the population densities of terrestrial birds. These authors noted that populations seem more variable if they are observed over a longer time period. This result is equivalent to the reddening of ocean variability discussed by Steele, but applied to population density. Again, the complex fluctuations of ecological populations could be thought of as a superposition of many simpler processes, some fast, some slow, each one acting on its own time scale. The rise in variance with observation time is a conse-

quence of seeing changes of slower processes that appear static on shorter time scales. Thus, even if the terrestrial environment is not reddened, terrestrial population abundances *are* reddened. Subsequent work set out to confirm or refute this for wider taxonomic groups (Ariño & Pimm 1995, Inchausti & Halley 2002) and for aquatic populations, both freshwater (Cyr 1997) and marine (Stergiou 1998, Halley & Stergiou 2005). Thus, for both marine and terrestrial populations, more time means more variance.

Pimm & Redfearn (1988) did not confine themselves to saying that variance sometimes increases with time. They implied that this increase was a universal trend irrespective of time scale and noted that their finding had 'implications for the debate over whether populations have an equilibrium' (Pimm & Redfearn 1988, p. 613). This is true, because 'cumulative variance ... must level off or be asymptotic' for population density to be bounded (Murdoch & Walde 1989, p. 120). An unbounded population density would imply that there is no real equilibrium and hence no regulation by density dependence. 'Regulation by density dependence', according to classical population ecology, refers to the way in which finite resources or overcrowding cause the population to remain close to an equilibrium. This

idea, naturally appealing and intuitive, turned out to be difficult to prove in the field. It has led to one of the most passionate (and at times bitter) debates in terrestrial ecology, between those who believe that populations were regulated by density dependence and those who thought they were regulated by the environment or not at all. For this reason, Pimm & Redfearn's paper was controversial (Greenwood 1989, McArdle 1989, Pimm & Redfearn 1989, Cyr 1997). It also marks something of a personal 'Damascus Road' for Pimm, who had earlier written that 'only a minority of populations fluctuate so wildly that an equilibrium level is not obvious' (Pimm 1982, quoted in Steele 1985, p. 355). However, in populations, although variance increases with observation time, there is also a tendency for the rate of increase to slow down (Fig. 1). Not all of Pimm & Redfearn's populations exhibited a continuing increase of variance: sometimes the variance appeared to reach a ceiling. Perhaps, the variance increase eventually stops so that population density remains bounded? Cyr, in particular, pointed out that, in contrast to the majority of populations described by Pimm & Redfearn, 'the inter-annual variability of most freshwater populations appears to reach an asymptote' (Cyr 1997, p. 556).

A continued growth of variance at longer time scales would have consequences for the types of models that ecologists should build. In the last decade, a substantial amount of theoretical analysis has been carried out in this area, to develop ecological models that yield the type of variance increases observed in real time series. Most of this work is by terrestrial ecologists (Table 1), and inherits the perspectives that dominate the density-dependence debate. Models fall into 2 basic categories: autoregressive models and power-law models. Autoregressive models are models in which a classical population dynamics model is combined with some 'buffer', such as age structure (McArdle 1989, Ripa & Lundberg 1996), acting to redden the dynamics. As well as being relatively easy to analyse, these models deliver the reassuring message that variability will stabilize eventually at some finite value. Alternative models tend to be based on the  $1/f$ -noise processes mentioned earlier (Halley 1996, Cuddington & Yodzis 1999, Morales 1999). These models are associated with fluctuations of population on all time scales. There is no fixed time scale associated with these processes other than the upper and lower limits of the observation process. According to these models there may be no limit to the growth in variance.

For most ecological time series, either terrestrial or aquatic, it is not possible to test the competing models, because given such short series the outputs of the different models are indistinguishable (Akçakaya et al. 2003). However, if some really long time series (for example, on time scales of millennia) could be found,

it would greatly contribute to our understanding. Sugihara (1995) analysed a terrestrial time series that stretches from the present back to the Tang Dynasty period in China: the record of migratory locust *Locusta migratoria* outbreaks over 1000 yr. Using this series for the locust, he confirmed Pimm & Redfearn's (1988) findings on a longer scale. However, because of the origins of this series, Sugihara's result might be vulnerable to criticism (i.e. that the data were not compiled in a scientific manner). Once again, it was aquatic ecology that provided a new avenue for progress. A chance meeting with Jeremy Jackson (Scripps Institution of Oceanography, San Diego, CA, USA) at a conference brought to my attention the existence of Baumgartner et al.'s (1992) reconstruction of Pacific sardine *Sardinops caerulea* and northern anchovy *Engraulis mordax* populations. Analyses of these 2 series revealed that, for these species at least, variance does continue to rise, even on scales of millennia (Halley & Stergiou 2005).

**Comparing the variability of terrestrial and aquatic populations.** Systematic differences between the terrestrial and marine environments should have consequences for population variability. Together with some colleagues, I have explored this conjecture (Inchausti & Halley 2002, Halley & Stergiou 2005). A first question to ask is whether the patterns of redness are similar. The Hurst exponent is a single index that measures the overall growth of variance with observation time (Ariño & Pimm 1995). If marine populations were more reddened, their Hurst exponents should be higher. However, the distributions of Hurst exponents for marine (e.g. fisheries landings) and terrestrial populations are virtually the same. It seems that while the 2 environments are very different, ecological populations, whether aquatic or terrestrial, have similar patterns of variance increase. Given that the 2 environments are so different, this similarity is surprising. However, there are also systematic differences. For example, at any given time scale, fisheries landings tend to be less variable than terrestrial populations. These comparisons illustrate some of the insights we can gain from large scale comparisons between the structure and function of aquatic and terrestrial ecosystems. For example, the broad characterisations for the variability of aquatic and terrestrial populations are useful. They might serve as 'neutral models' against which to test ecological theories (neutral models are often used, e.g. in economics, as a type of null hypothesis against which to test theories; Ginzberg & Jensen 2004). Also, large scale comparisons permit us to understand both systems more deeply. For example, comparisons between 2 systems with such different patterns of variability required new tools (e.g. spectral redness, Hurst exponents, and fractals). These tools, in turn, provided fresh insights, such as the connection between population regulation and variance growth.



**Is temporal scale more of an issue for terrestrial ecologists?** Our understanding of temporal scale in ecology, and its connection with redness and variability, has improved considerably in the last 2 decades due to vigorous research in the area. It is indisputable that this research also owes much of its vitality to the inspiration of a number of compelling ideas that originated in aquatic ecology: that scale is a useful concept, that the redness of environmental variability matters, and that we should make large scale comparisons between aquatic and terrestrial systems. But is this issue now less interesting for aquatic than terrestrial ecologists? Table 1 shows some of the important publications on this topic and the ideas introduced. It also shows whether each team included aquatic ecologists and whether the publication was in an aquatic ecology journal or book. While both marine and freshwater ecologists are well represented in this field (in 11 of the 18 papers), the same is not true of aquatic ecology journals. Although some of the seminal ideas in this area were published in journals or proceedings of marine ecology, most have been published in general ecology journals. With modern search tools there is no serious problem of access to potentially relevant articles in journals of aquatic ecology, but this was not true 20 yr ago. Given that terrestrial ecologists have tended not to browse through journals of aquatic ecology, it is likely that freshwater or marine ecologists prefer to publish in journals of general ecology those ideas likely to be of general interest. How different might have been the history of this subject if Steele, and Steele & Henderson, had published only in aquatic journals? Out of the 24 papers explicitly mentioned in Table 1, only 5 are from specifically aquatic journals or books. Then again, only 1 of the other 19 papers is from an exclusively terrestrial journal. So while temporal scale remains a big issue for all ecologists, the forum of research is now perceived to lie in the field of general ecology rather than either terrestrial or aquatic ecology. Perhaps, journals of aquatic ecology are seen as being a somewhat specialized genre both by terrestrial ecologists and by aquatic ecologists themselves.

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## Cross environment talk in ecology: fact or fantasy?

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**Introduction.** I will argue that ecology with its roots in 'natural history,' whether that was stalking prey, keeping special mushroom (e.g. morel or truffle) sites secret, or the best spots to fish, was initially an individualistic endeavor. Deep knowledge of parts of the natural world was a requisite for survival. Dayton (2003) studying kelps, and Greene (2005) investigating snakes, deplore our continuing ignorance of ecology and behavior, i.e. the natural history, of most species. The problem is surely greater for marine biota than for the more observable and accessible terrestrial ones; the shadow cast by this collective ignorance is central to any understanding of the effectiveness of communication between ecologists, and even of the degree to which they communicate, irrespective of their study system of choice. If one has no sense of the badger's or vicar's role in Elton's (1927) analogy, how can one compare ecosystems, except on a purely numerical (e.g.  $gC\ m^{-2}\ d^{-1}$ , standing crop biomass as  $kg\ m^{-2}$  or  $m^{-3}$ , or species richness as  $H'$ ) basis? If one lacks a feeling or 'gestalt' for the individual species or even trophic group, discussion is certain to focus on numerical rather than intimately biological similarities or differences.

The plausible terrestrial/marine dichotomy has at its core the obvious differences in major taxa: fishes vs. birds, crustaceans vs. insects, algae vs. higher plants. Fundamental differences in the viscosity of the respective media (air vs. water) dictate further patterns in taxonomic composition, life history traits, physiology, movement, etc. Many marine benthic systems are dominated by sessile animals. There are no terrestrial counterparts, without broad leaps of faith. Recruitment issues often characterize interpretations of marine population dynamics; the term seems foreign to terrestrial ecologists. Conversely, pollination is a fundamental and mainly terrestrial process. Carr et al. (2003) have listed the major differences between marine and terrestrial ecosystems, and I see no need to duplicate that effort. Prominent, however, is the relative openness of marine

systems with the implied magnification of spatial scales due to the effectiveness of long distance dispersal.

To evaluate the questions posed for this *MEPS* Theme Section, I have used as my reference state marine, rocky near-shore ecosystems, where space on which to attach and grow is arguably the most significant resource, mortality due to predation or disturbance is obvious, even commonplace, and experimental manipulation of many component species relatively easy. Thus manipulative tractability, especially of higher trophic levels, is my primary theme. A secondary one, but arguably of equivalent importance, is the historical division of all ecology into basic and applied camps. This separation, nurtured by differences in graduate training, society membership, funding sources and research focus, has effectively disguised whatever commonalities in ecological process and system response might exist.

**The consequences of 'big science'.** Ecology until fairly recently tended to be a solitary profession; one did one's research alone and took credit or blame accordingly. That has changed. I assume that a transition to 'bigger' science has increased the dialogue within research programs, but probably at some cost to innovation. Some evidence supporting my contention of developing bigness is illustrated in Fig. 2: the highly significant trend towards a diminishing frequency of sole-authored papers in *Ecology* since its inception in 1920 through 2004. The figure entries represent my assessment of what fraction of the papers in the first issue of each volume year had a single author; some judgment calls were necessary and I have excluded commentaries, book reviews, reports and the very few obituaries. One obvious cause of the growing tendency towards multi-authored papers is that some problems are so cosmic that teams of experts are required to tackle the issue. Genome sequencing, climate change, and sea level rise come to mind. But has this bigger,

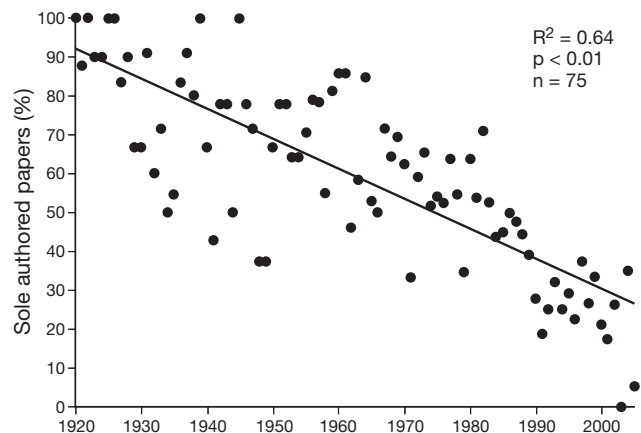


Fig. 2. Declining frequency of single-author research papers in the first issue of each volume of *Ecology*, from 1920 to 2004

often lavishly funded version of science increased the 'cross-talk' between terrestrial and marine ecologists? I doubt it; in fact inter-group communication may have diminished as large programs tend to be goal oriented and dominated by a necessary 'group think' or 'good team player' philosophy. A cynical explanation is that continued funding, rather than hypothesis exploration, is the primary goal.

**Traditional barriers.** Two classic 20th century studies illustrate nicely that barriers to communication may lack an environmental component. The Hairston et al. (1960) paper on the trophic organization of terrestrial systems immediately attracted foes and supporters. Its primary thesis that producers and carnivores tend to be resource limited, while herbivores are predator limited, remains controversial. However, it anticipated my 'trophic cascade' hypothesis (Paine 1980) by 2 decades and would have been compatible with many current models of community organization, if the dominating influence of mammalian grazing (rather than that of insect herbivory) had been considered (Paine 2000). The presence of cascades is routinely demonstrated in aquatic systems subject to top-down forcing (e.g. Estes & Palmisano 1974, Power et al. 1985, Carpenter & Kitchell 1993, Silliman & Bertness 2002) and is increasingly discovered in terrestrial systems (e.g. Schmitz 2003, Van Bael et al. 2003; for a meta-analysis, see Shurin et al. 2002). Nonetheless, cascades remain unknown or unrecognized in many ecosystems subject to potential top-down forcing, and Strong's (1992) humorous caveat remains in force.

The second 20th century classic work is that of Brooks & Dodson (1965). I have often claimed in seminars (though never in print) that many biological oceanographers may have read and then forgotten or simply ignored its sweeping implications. Their message, however, was unambiguous: trophic dynamics in a top-down sense can influence patterns of species composition in communities, and thus, ultimately, primary production. One can argue that ecological extrapolation from a small freshwater pond to the enormous expanses of marine pelagic assemblages is unwarranted. Fair enough, but the top-down dynamics illustrated by Worm & Myers (2003) and Shiimoto et al. (1997) suggest that dismissing the possibility—in the absence of interest or data—is inappropriate.

Finally, there are unfortunate but traditional barriers to communication between 'basic' ecologists—usually housed in colleges of arts and science—and their cousins in 'applied' departments. Managers of grazed grasslands and forests, and individuals charged with governing industrial fisheries have often assembled and carefully archived massive amounts of information, much of it bearing the hallmarks of ecological utility that their academic counterparts aspire for: for

instance, lengthy time series, single stock demography, and community response. This barrier seems to be dissolving, at least for marine systems, following the realization that many stocks of sharks (Ward & Myers 2005) and bony fishes (Pauly et al. 1998, Myers & Worm 2003) have been substantially over-exploited. While these conclusions have been challenged (Hampton et al. 2005), I believe the resultant literature exchanges between academic and government scientists to be a healthy development.

This connection is recent and driven by growing concerns about the environmental impact of industrial fisheries. Issues such as appropriate baselines (Jackson et al. 2001) against which declines can be calibrated or recovery goals established can draw information from fields as divergent as history and fisheries ecology. Equally, concerns about 'fishing down the food web' (Pauly et al. 1998) have sharpened debate on whether traditional single stock management should be supplanted by a more general and ecosystem based approach. The complexities inherent in this latter perspective have deep roots in small-scale experimental ecology.

**Where trans-system communication thrives.** Terrestrial ecosystems and their inhabitants present substantial challenges to investigators: many species potentially outlive researchers by decades; powerful and appropriate legal and moral constraints exist on manipulating (and therefore understanding) the dynamical roles of such protected species as birds and grazing mammals, or even in whole ecosystems such as old-growth forests. In contrast, there are no politically active lobbies for starfish, barnacles, tunicates, bryozoans or even kelps. Thus if the dichotomy proposed for this MEPS Theme Section had been experimentally tractable vs. intractable natural systems, a convincing pattern would have emerged. Rocky shores and a variety of freshwater ecosystems ranging from ponds (Carpenter & Kitchell 1993) to small rivers (Power et al. 1985) would bin comfortably into one category, oceans and most terrestrial landscapes into another. My impression is that the experimentalists talk to, and criticize, one another (Hairston 1989, Resatarits & Bernardo 1998). I cannot think of any examples of discussion or relevant literature on the common problems introduced by immense spatial scale and experimental intractability, say by oceanographers and foresters.

On the other hand experimental manipulations at small spatial scales are routinely conducted. Their focus is often an exploration of the growing host of anthropogenic ecological mischief. The literature cited in these papers overlaps substantially. The common denominator for such studies is manipulation and the derived insights, not a common environment.

Three examples follow:

(1) Invasive species are increasingly common in most ecosystems and much of their impact is detrimental. Interest has focused, beyond detection, on whether they might destabilize a system or irrevocably alter its functioning. Levine (2000), studying a riparian but primarily terrestrial system, showed that the most diverse natural assemblages were invaded most frequently. Diversity manipulations and seed addition experiments supported this finding. A comparable study by Stachowicz et al. (2002), conducted at depths from 1 to 10 m on a sessile marine fouling community, also tested experimentally hypotheses based on the interactions between resident diversity and site invasibility. Conversely, they found that more diverse systems were invaded less frequently. Both studies are convincing and although their conclusions differ, the later marine paper cited 50% (15 of 30) of the other paper's references. Experimentally based hypothesis testing fosters, even requires, such overlap. While it is perhaps not communication in the strict sense, it does represent an intellectual bridge that is independent of environment.

(2) Terrestrial ecologists are increasingly concerned about the impact on assemblage function or even persistence of rampant extinctions, particularly in the tropics. Documented extinctions in marine shallow water ecosystems can be counted on 1 hand. Has this striking difference polarized research on how changes in species richness influence assemblage functioning or persistence? I believe the answer to be 'no.' The sophisticated experiments initiated by Tilman and extended by Loreau, Naeem and others (see review by Hooper et al. 2005) probably cannot be repeated in any marine system: recruitment in such open systems is unpredictable, and a 'transplanting' technology is minimally developed. However, their 'consensus of current knowledge' represents a terrestrial opinion, and one based on within-trophic-level manipulations (generally of grassland species). Notably, the Mulder et al. (1999) insect removals almost doubled plant biomass production, a change more than 6 times greater than the changes produced by varying plant species richness. Parallel marine experiments have also focused on alterations of trophic pressures (Duffy 2002, Paine 2002). The resultant massive, experimentally-induced shifts in net primary production have not escaped the attention of terrestrial researchers, leading Hooper et al. (2005, p. 15) to recommend that 'greater experimental efforts at understanding multitrophic changes in diversity constitutes a clear need for future research.' Such cross-fertilization seems common in experimentally tractable systems, and appears generally independent of environment.

(3) There is a growing awareness that one ecosystem can subsidize or influence another: iron-rich African

dust can fertilize the South Atlantic, forests add carbon to rivers, etc. But systems can be linked trophically as well, as Silliman & Bertness (2002) have convincingly demonstrated. Salt marsh meadows are arguably the most productive ecosystems in the world, and yet population explosions of a marine snail seem to control their luxuriance. Experimental exclosures were employed to protect a grass (*Spartina alterniflora*); snail inclosures reduced such meadows to barren mudflats within 8 months. A plausible explanation of the phenomenon is that commercial over-exploitation of a pelagic crab, a major snail consumer, allows snail density to increase, resulting in devastation of the marsh. It is unknown and minimally investigated how common trophic supplementation, or reduction, in one community influences another. For instance, increasing populations of snow geese fed on corn during winter are in the process of destroying aquatic vegetation on their nesting grounds in boreal Canada (Jano et al. 1998). Choi et al. (2004) have suggested that recovery of benthos-feeding cod stocks in the NW Atlantic may be inhibited by compensatory increases in pelagic fish populations. Manipulation of nutrient and trophic subsidies is already within the experimentalist's toolbox, suggesting that eventually the character of the impacted interactions rather than environment will provide the basis for synthesis.

**Conclusions.** A pessimistic view is that as ecology moves inexorably towards 'bigger' science, the traditional barriers to communication will be magnified, not reduced. A terrestrial-marine disconnect is one such barrier; the 'basic' vs. 'applied' dichotomy remains a more fundamental one. However, the design of small-scale experiments often requires some intimacy with the target species' natural history. This necessary focus on organisms and the implied experimental probes of nature's organization and complexity has generated a style of ecology in which the question, not the environment, plays a dominant role. Communication within this subset of ecologists, and its reciprocal influences, is perhaps not widespread, but it is commonplace. If cross-environment communication is to be increased and barriers are to be reduced, I believe it will best be achieved from the bottom-up, that is by building on the accumulated wisdom about individual species and the consequences of their interactions.

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## Do marine and terrestrial ecologists do it differently?

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**Introduction.** Differences between marine and terrestrial ecologists in the way they go about their science are rooted in the departmentalism that is reflected in the structures within institutions and educational systems (Max-Neef 2005). Thus, within ecology we can recognise the sub-disciplines of molecular, plant, animal, marine, terrestrial and freshwater, physiological, theoretical, population and ecosystem ecology. Bridging departmental boundaries is challenging, but there are major gains to be had in terms of learning and importing ideas from other disciplines, as well as generating novel research areas which cut across existing paradigms and ways of thinking. This often requires a different individual mindset than is currently produced by western education systems, which have become increasingly reductionist and oriented towards specialised training, often reinforced by the local distinctiveness of undergraduate training programmes (Max-Neef 2005).

In the United Kingdom there were 108 distinct marine and 470 distinct ecology undergraduate degree programmes available at Universities for 2005 entry ([www.ucas.ac.uk](http://www.ucas.ac.uk)). These programmes have their own distinctive flavours, the curricula reflecting the interests and expertise of the staff responsible for delivery and a desire to differentiate in a competitive market. For instance, one marine science programme may have substantial elements of mainstream ecology, other programmes will have very little. Similarly, an

ecology programme at one institution may be dominated by marine themes, whilst these would hardly feature at all at another institution. Because much of the curriculum is derived from the interests of those staff responsible for delivering the teaching, and is dominated by staff in their 40s and 50s, who are likely to have been educated in a mono-disciplinary system, departmentalism is perpetuated.

There is a real desire, particularly among younger researchers, to take an inter-disciplinary approach, but substantial barriers remain. These barriers include

- Unsympathetic and unresponsive mono-disciplinary audiences for both oral and written presentations—journals, editors, reviewers and learned societies are still mainly mono-disciplinary. This presents a challenge for those evangelising outside their own discipline. Missionary attempts are often met with hostile rejection.
- Difficulties in securing funding, given the mono-disciplinary nature of most national research funding councils. For instance, until relatively recently the UK's prime funding agency for environmental research had separate review panels for marine, terrestrial and freshwater ecology, frustrating attempts at research that bridged these systems.

We are optimistic about the future, but historically marine and terrestrial ecology have diverged along quite different paths in a number of areas. It is not clear whether the differences that marine and terrestrial ecologists perceive in the ways that marine and terrestrial systems are structured and function are real, or the product of departmentalism. Do the 2 disciplines view fundamentally similar ecological systems through different sets of educational and institutional filters? It is important to determine whether these contrasts are real or imagined, given the imperative to address global-scale issues such as climate change, where links and feedbacks between terrestrial and marine systems are readily acknowledged but poorly investigated and articulated (Gattuso et al. 2005).

In this paper, we first consider the unambiguous and very real differences which exist between the nature of marine and terrestrial systems, and then we explore a few examples of the different ways in which marine and terrestrial ecologists have approached key areas within ecology: biodiversity and ecosystem functioning, food web and ecosystem ecology, and macroecology—as well as the benefits accrued when these boundaries have been crossed. Finally, we ask whether the different approaches taken by marine and terrestrial ecologists to these major themes reflect real differences between the 2 types of ecosystem, or cultural differences generated by many years of departmentalism.

### **Contrasts between marine and terrestrial systems.**

Marine and terrestrial systems differ in a number of key physical and chemical characteristics which have influenced the evolution of their respective biota (Link 2002, Carr et al. 2003, Nybakken & Bertness 2005). The properties of sea water, in particular its density and viscosity, have resulted in ecological communities (e.g. the plankton) and life styles (e.g. filter feeding) unknown on land (Denny 1990, Vogel 1994). Likewise, differences in the availability of light, oxygen and various key nutrients have driven the evolution of quite different plant taxa and assemblages in marine compared to terrestrial systems (Nybakken & Bertness 2005), as a result of which certain common terrestrial life forms (e.g. pollinating insects) are absent from the sea.

These differences are unambiguous and real, but others may reflect differences in perception. For example, the degree to which communities are assembled and structured by stochastic, external, physical processes, rather than by intrinsic biological rules, in marine and terrestrial systems. Marine biology textbooks emphasise the need to appreciate the large-scale circulation of the oceans in order to understand the dynamics of local communities (e.g. Nybakken & Bertness 2005). Thus, widespread passive dispersal in the plankton, combined with variation in environmental variables on short timescales, is thought to lead to a lack of isolated communities with reduced levels of endemism compared to terrestrial systems (e.g. Steele 1985, 1991, Carr et al. 2003, Nybakken & Bertness 2005), although restricted-range endemics do occur (e.g. Hughes et al. 2002, Roberts et al. 2002). Even relatively static marine communities, are thus seen as remaining essentially 'open', their composition largely determined by whichever planktonic larvae happen to be in the right place at the right time. In contrast, terrestrial systems are often portrayed as conforming to rules for the assembly of communities, a more ordered ecological succession, and higher levels of specialisation and endemism (e.g. Steele 1985, 1991, Wiens 1989, Carr et al. 2003, Irigoien et al. 2004). Even intertidal systems are essentially open (Hawkins 2004).

This distinction between marine and terrestrial systems is highly dependent on the spatial and temporal scale at which comparisons are made (Wiens 1989, Steele 1991). For example, terrestrial ecologists appreciate that the structure of local communities is constrained by the regional species pool, which will be strongly influenced by processes operating at large spatial and temporal scales including plate tectonics, large-scale climate change, and simple chance (e.g. Wiens 1989, Taylor & Gotelli 1994, Webb & Gaston 2003, Qian & Ricklefs 2004). In addition, neutral models of community assembly developed in terrestrial

systems (e.g. Hubbell 2001) require the ecological equivalence of all individuals (i.e. no tradeoffs between colonisation and competitive ability, no niche differentiation). In addition, terrestrial ecologists are increasingly recognising the more immediate impacts of external environmental forcing (e.g. El Niño, North Atlantic Oscillation) upon ecological dynamics across multiple spatial scales (e.g. Holmgren et al. 2001, Ottersen et al. 2001). The perceived differences between marine and terrestrial ecological processes are less obvious considered at these different scales.

We recognise differences in approach between marine and terrestrial ecologists in 3 areas:

**(1) Biodiversity and ecosystem functioning:** Understanding the relationship between species diversity and key ecological processes has become one of the most pressing themes in contemporary ecology (Loreau et al. 2002, Hooper et al. 2005). But the vast majority of the literature in this area emanates from terrestrial plant and soil ecology. This is despite direct appeals to the marine research community to enter this arena (Emmerson & Huxham 2002, Raffaelli et al. 2003), and despite the similarity of processes across biomes (Belgrano et al. 2002, Covich et al. 2004, Gray et al. 2006) and the publication of several influential marine studies that have been placed firmly within the biodiversity-function framework (Duffy et al. 2001, Emmerson et al. 2001, Bolam et al. 2002, Lohrer et al. 2004, Solan et al. 2004, Waldbusser et al. 2004). Is this difference in research effort linked to historical and/or cultural differences (i.e. lack of a common language, specialization of publication venues, and so on; Turner & Carpenter 1999, Raffaelli et al. 2003), or to a more fundamental division in scientific opinion over the validity and importance of biodiversity-function hypotheses in the 2 systems?

The introduction of a new paradigm is often met with dismissive contempt, and initial attempts to articulate related hypotheses can be heavily criticised; such is the scientific process. Nevertheless, revisiting ecological theory has been the mainstay of recent advances in benthic ecology as contemporary perspectives merge with older and more familiar conventional ideology (e.g. organism-sediment relations; Gray 1974, Rhoads 1974). Yet these particular contemporary and older paradigms are remarkably similar in many ways. Both consider the relationship between organism and sediment, measure similar benthic processes (bioturbation, nutrient flux) and both infer similar implications for ecosystem functioning along environmental gradients. Some critics have, therefore, concluded that the consideration of biodiversity-function issues in marine benthic systems is tautological and that benthic ecology is reinventing itself (Flint & Kalke 2005), rather than investing and building on prior knowledge (Em-

merson & Huxham 2002). However, it is important to recognise that despite apparent similarities to past work in this area, not least in terminology and data requirements, modern treatments are often subtly different from previous ones (Raffaelli et al. 2005). Whereas biodiversity has been traditionally treated as a response variable, contemporary syntheses have recognised the functional significance of the biota and treated biodiversity as an explanatory variable (e.g. Emmerson et al. 2001). This historical difference in emphasis contributes to a disagreement about the importance of biodiversity for ecosystem functioning in the 2 ecosystems. We believe that the relationship is similar in marine and terrestrial systems, so that the perceived differences are largely cultural.

**(2) Food webs and ecosystems:** Ecologists have traditionally formalised the complex relationships in ecological systems as trophic networks or food webs, depicting the arrangement of linkages and the flows of materials between species. Some of the earliest well-documented food webs were marine, such as Alistair Hardy's (1924) classic depiction of the sink web of the herring *Clupea harengus*. Also, the paradigm-setting manipulative field experiment approach designed to unravel the dynamics of food webs were also largely marine (Paine 1980, and references therein). However, several other recent developments in food web ecology have not been embraced by marine ecologists, including the area of food web theory. This field involves deriving vital statistics of food webs from their binary representations of who eats whom, including: the number of species, the number of links and their various products such as linkage density and connectance, the number of linkages from basal to top species (food chain length), the proportions of different kinds of species (top, basal, intermediate and omnivores), as well as more esoteric features such as triangularity and rigid circuits (Hall & Raffaelli 1993). Such statistics have been derived (but not by marine ecologists—see below) for a wide range of marine, freshwater and terrestrial food webs, and from constant as well as from fluctuating environments.

The food webs analysed in this way are drawn from terrestrial and aquatic systems, but food web theory has largely been the preserve of mainstream ecology, which is dominated by terrestrial ecologists, as reflected in publication outputs. Of the 25 key primary papers in this field (excluding reviews and books) found in a Thomson ISI Web of Knowledge search of 'food web patterns (July 2005)', only 1 is from a researcher (D. Raffaelli) vaguely recognisable as a marine ecologist. This is probably because few marine ecologists would view food web structure and underlying dynamics from this perspective. Many marine

ecologists view size-based, rather than species-based interactions as more appropriate ways for exploring marine trophodynamics (Raffaelli 2005; see below). In other words, the difference in approach to food webs by marine and terrestrial ecologists may reflect fundamental differences in the way marine and terrestrial systems are organised. Alternatively, size-based approaches may be long overdue in terrestrial food web ecology (Raffaelli 2005).

In contrast, the system approach to trophic networks is dominated by marine ecologists. One of the ways in which trophic structure and behaviour can be explored is through the use of mass-balance models and network analysis, and tools such as Ecopath (Christensen & Pauly 1992) are readily available and provide accessible frameworks for the systems approach to trophic ecology. Interest in ecosystem ecology is clearly alive and well—an ISI Web of Knowledge search provides over 27 000 hits for the term 'ecosystem'—and there are far fewer publications (July 2005) which take a classical thermodynamics-oriented approach. However, more than twice as many references to mass-balance approaches were from marine ( $n = 46$ ) than from terrestrial (20) studies, but only 1 out of 46 papers which used Ecopath as a systems ecology tool was terrestrial. When the search term 'thermodynamic' was added, there were 8 marine and 2 terrestrial papers identified. These data confirm our impression that systems ecology is better represented in marine as opposed to terrestrial fields, probably for historical reasons (systems ecologists tend to publish in different journals and attend different conferences, and marine environments have often been the systems of choice), rather than because of any real differences in the way marine and terrestrial systems are organised and function. Indeed, Eugene Odum's (1953) tome, *Fundamentals of Ecology*, is an attempt to use systems approaches as a general unifying framework for ecology, both terrestrial and aquatic.

**(3) Macroecology:** The most fundamental differences and the broadest similarities between marine and terrestrial systems are likely to emerge at large spatial scales. This is the domain of macroecology. The marine environment presents particular practical, logistical and financial challenges that make the type of datasets relied upon by terrestrial macroecologists (often compiled through the efforts of committed volunteer naturalists) difficult to obtain for marine taxa. As a consequence, macroecology remains over-whelmingly a terrestrial subject. Thus, <10% of ca. 300 papers indexed by Thomson ISI Web of Knowledge which contain the words 'macroecology' or 'macroecological' in the title, keywords or abstract, are analyses of marine systems (July 2005).

In addition, defining variables crucial to macroecological analyses in marine systems, such as 'range size' and 'population size', can be problematic, particularly for pelagic taxa or for regions with (often highly) incomplete sampling. For instance, many macroecological studies on birds are based on thorough sampling of hundreds or even thousands of relatively large sampling units (e.g. 10 km squares). The effective area sampled by marine macroecological datasets, even when they have been compiled over similarly extensive areas, is usually far less, with the notable exception of fisheries data. Nevertheless, the increasing availability of suitable marine datasets has stimulated basic macroecological investigations into marine taxa (44% of the ca. 300 macroecological studies identified from Thomson ISI Web of Knowledge have appeared since 2004), and recent novel applications of macroecological techniques and interpretations of macroecological patterns have originated in marine systems (e.g. Li 2002, Fisher & Frank 2004, Jennings & Blanchard 2004, Frank et al. 2005), in part due to the problems inherent with marine data.

Simple investigations of frequency distributions of single macroecological variables (see below) have revealed certain generalities between marine and terrestrial taxa. For instance, species–range size distributions display a characteristic right skew for both marine and terrestrial taxa (Gaston 2003): most species have restricted distributions, only a few are widespread. Similar patterns are also seen for species–abundance distributions: Gray et al. (2006) show that these are of similar form (good fit by 2 lognormal distributions) in a variety of marine and terrestrial taxa. Importantly, Gray et al. (2006) restricted their terrestrial analyses to datasets sampled under a regime similar to the one typically employed in the marine environment, i.e. samples from an assemblage of unknown species richness. 'Typical' terrestrial datasets where it is possible to ensure complete enumeration of individuals may show a rather different form (Williamson & Gaston 2005). This suggests that some of the apparently unusual features of marine species–abundance distributions, for instance the prevalence of many species which only occur once in the sample (singletons), may be due to differences in the way marine and terrestrial systems are sampled.

Investigations of a third principal macroecological variable, body size, have progressed somewhat differently in marine and terrestrial systems. Whilst the distribution of body sizes between taxa is seen as an important indication of the way that resources are utilised in ecosystems (as well as the constraints imposed by the environment and phylogeny), marine and terrestrial ecologists differ crucially in whether



they consider body size to be a fixed entity (adult body size or mean body size) or a continuous function. We have argued elsewhere (Raffaelli 2005) that this difference in perspective affects the way ecologists view food web structure and dynamics. In both marine and terrestrial systems, smaller prey are eaten by larger predators (Cohen et al. 1993), and both predators and prey change (increase) their body sizes over time (note: this only applies in terrestrial systems to animal predators and their animal prey). These continually changing size distributions are formally acknowledged in the biomass spectra approaches taken by marine and freshwater ecologists, where the relative size of living particles is the predominant driver of trophodynamics. Aquatic food chains are simply ways of making larger packages of energy to fuel the trophic level above. Size-dependency in predator–prey interactions is well understood by mainstream ecologists (e.g. Cohen et al. 1993), but we know of no documented biomass spectra for terrestrial systems equivalent to those which exist for marine systems. This is an area where terrestrial macroecologists can learn from marine ecological theory.

As macroecology continues to develop as a discipline, its emerging theories will benefit from being tested in as many environments as possible. Indeed, given the practical constraints to an experimental approach at these scales, comparisons between environments may prove the most powerful tests of proposed mechanistic hypotheses. Particular aspects of the marine environment that will be useful include strong environmental gradients (e.g. with increasing depth), as well as the vast taxonomic diversity (in particular at higher taxonomic levels) found within marine communities. The use of macroecological techniques by marine ecologists to address questions such as the impacts of fishing on body size–abundance and abundance–occupancy relationships (Fisher & Frank 2004, Jennings & Blanchard 2004) suggests that the required cross-fertilisation of ideas and techniques is already occurring.

**Conclusions.** Some of the clearest and most compelling demonstrations of ecological principles come from marine systems, especially shallow water environments—e.g. Bob Paine’s research on keystone species (Paine 1980)—but there is no doubt that the discipline of ecology has been profoundly influenced by the findings and personalities of terrestrial ecologists, such as Charles Elton and Arthur Tansley. For example, despite the ground-breaking work of marine ecologists referred to above, there were no marine (or freshwater) contributors to a jubilee celebration of what progress had been made in the key concepts in ecology (ecosystems, food webs, niche, diversity–stability, predator–prey dynamics, population

regulation, competition, life history strategies, optimization) over the 75 yr since the founding of the field by the British Ecological Society (Cherrett 1988). Similarly, the companion volume on anticipated new developments in ecology (Grubb & Whittaker 1989) contained only 1 marine contributor out of 18 (the systems ecologist Bob Ullanowicz). This implies that mainstream (terrestrial) ecology, at least at that period, had not felt the need to connect with much of marine ecological research.

The terrestrial domination of mainstream ecology remains a feature of the discipline today and contributes to the departmentalism that makes bringing novel concepts into marine ecology so challenging. A consequence of this departmentalism is that marine and terrestrial ecologists attend different conferences, publish in and read different journals, and use their own technical jargon, so that each discipline is often unaware of developments in the other. Yet each could learn so much from the other. For instance, marine ecologists have long been working on the linkages between biodiversity and ecological functioning in benthic systems, have an excellent understanding of the effects of bioturbation on biogeochemical processes and are well able to measure these processes in difficult environments (Raffaelli et al. 2003, Solan et al. 2004). But as a community they have generally failed to appreciate and incorporate the emerging paradigms from mainstream ecology that would have enabled them to make significant progress in this area (Ives et al. 2005). Conversely, improved understanding of population and community dynamics in terrestrial systems has been gained by using mass-balance approaches developed for marine systems (Ruesink et al. 2002). In addition, innovative applications of macroecological theory, driven initially by terrestrial ecologists, have recently been developed by marine ecologists (Li 2003, Fisher & Frank 2004, Jennings & Blanchard 2004).

There are numerous examples which illustrate the potential for improved understanding of ecological systems by cross-fertilisation of marine and terrestrial ecology. More important perhaps is identifying the mechanisms which would lead to better interdisciplinary activity. Researchers can improve interdisciplinary science through the use of conceptual models as a communication tool (Heemskerk et al. 2003), but one of the most effective mechanisms for promoting cross-fertilisation across the disciplines is to provide funding which encourages different disciplines to work together. Unless such opportunities exist, researchers will tend to remain within their mono-disciplines, where peer recognition, research performance indicators and grant income streams are more safely assured.

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## Uniting ecologists into a smooth, tasty and potent blend

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**Introduction.** While most whisky lovers prefer single malts rather than blends, the sciences typically taste best when mixed. Interdisciplinary teams will always have a broader spectrum of background knowledge and competence than will be available within single discipline teams. In particular, we argue that a combined marine and terrestrial team will perform better than either purely marine or purely terrestrial groups. This is so, because in mixed teams specialists from each of the fields will mutually fertilize each other with concepts and approaches. In the following, we provide some examples from population ecology, showing how we (and others) have benefited from mixing across the borders between the 2 types of ecosystem, and then we discuss how such integration could be implemented to

greater effect. For instance, terrestrial ecologists emphasize the presence of density dependence more than marine ecologists, and conversely, marine ecologists may teach their terrestrial colleagues about effects of large-scale climatic features such as the North Atlantic Oscillation (NAO).

**The relative role of limiting factors.** Insights from different ecosystems typically broaden our views and, most importantly, make us realize that generalizing on the basis of single-system studies might be rather inadequate. One of the classical controversies in population ecology is what regulates population abundances and the temporal variation in population size—the intrinsic, density dependent factors (DD; Nicholson 1933) versus extrinsic, density independent factors (DID; Andrewartha & Birch 1954, reviewed by Turchin 1995). Much of this apparent controversy arose because the scientists involved generalized to all ecological systems after studying rather specific ones—some using insects in arid terrestrial systems (Andrewartha & Birch 1954), others studying small mammals in temperate terrestrial systems (Nicholson 1933). Both were at least partly right for their own system—but individually they represent end-point conditions of a continuum. Today—after combining insights derived from studies in a variety of ecological systems—no one would claim that it is a matter of either DD or DID. Rather, today we know that both DD and DID factors are important and that they typically interact with each other. In a marine context, much focus has been on temperature and advection by ocean currents (i.e. DID factors) and much less emphasis has been placed on DD factors, while in terrestrial ecosystems for a long time the opposite was true (see below). When one of us switched from working primarily on rodents within a DD framework (e.g. Stenseth 1999) to various population dynamics issues in a marine setting, much of the same principles, but differing in importance, were apparent in a marine context (Lekve et al. 2005).

Predators may be affected by annual availability of prey in 2 contrasting ways; either due to annual variation in (overall) abundance, or in the timing of when the prey are available relative to breeding phenology of the predator. The latter is referred to as a trophic mismatch (Cushing 1990). Later a similar concept was, without a link to the marine literature (Stenseth & Myrseth 2002), presented for terrestrial systems (Visser et al. 1998, Visser & Holleman 2001). Recently, we applied the match–mismatch hypothesis to marine (cod/zooplankton), marine–terrestrial (herring/puffin) and terrestrial (sheep/vegetation) ecosystems (Durant et al. 2005). We thus generalized the match–mismatch concept and learned that the timing component might be the more important in a marine setting, while the abundance component might be the more important in

a terrestrial setting. Through the mixing of expertise from both marine and terrestrial systems, we have learned more ecology than we would have otherwise: the marine and the terrestrial systems may be seen to represent end points of a continuum, an insight difficult to obtain unless similar work is carried out on both systems.

**Cultural enhancement of initial differences in ecology.** Marine and terrestrial ecology move forward along separate paths. It takes much effort and time to master each of the 2 fields, to ask pertinent research questions, and to perform good experiments. Consequently, it is difficult for scientists to switch between systems. In addition, we feel (on the basis of personal experiences by some of us) that there is, as in other disciplines, a great deal of subtle resistance against 'intruders' wanting to switch fields of interest—for instance, from terrestrial to marine. Funding options are typically also quite different, national research councils often have separate marine and terrestrial programs. There are few programs under which marine and terrestrial ecologists can meet—and compete for funding.

**Data collection issues.** Different ecosystems normally differ in the way they appear (e.g. a forest looks different from the ocean). Less obvious is the fact that, for ecologists, terrestrial and aquatic ecosystems differ fundamentally in the type of data that can be easily collected to study them. While it is easy for theoretical ecologists to demand various types of information for answering a given ecological question, practical and economic limitations may prevent certain types of data from being acquired. For example, it is easier to obtain individual-based, long-term capture-mark-recapture data from terrestrial systems. On the other hand, knowledge of marine ecosystems is based—to a larger degree than in the case of terrestrial ecosystems—on data collected at greater spatio-temporal scales, such as fish catch statistics and SAHFOS (Sir Alister Hardy Foundation for Ocean Science; <http://192.171.163.165/>) Continuous Plankton Recorder (CPR) records. The analysis of individual-based ecological processes may, therefore, be accomplished more easily within a terrestrial system whereas the study of long-term fluctuations might be more easily done within marine systems. Although both types of studies are conducted on both categories of ecosystems—methods are developed along somewhat separate paths, since the data structure reflects the collection methods. Cross-system collaboration would certainly benefit both marine and terrestrial ecologists. For example, telemetry techniques have long been widely used both in marine and terrestrial studies (Jouventin & Weimerskirch 1990, White & Garrott 1990, Priede & Swift 1992), and are now used more and more often also for marine studies (e.g. Åkesson 2002).

**Scales of perception.** Researchers are not only products of their scientific and theoretical training, but to a large extent also of the ecological systems they work on; this is again linked to the type of data that can be obtained, and hence to the type of questions that can be asked and answered (see above). The world is also perceived differently from a ship struggling through the white waves of the Northern Atlantic than from under a spruce tree in the deep forest. For example, when you are getting wet and cold while tracking animals in the snow and see how they struggle for survival, you really understand the need for data on precipitation and snow depth at those sites that are assumed to be of importance for quantifying how climate affects the performance of terrestrial organisms. The marine habitat is less accessible to humans and so we lack such 'hands-on' experience. Because of the extensive distribution of many marine populations, the population data are derived from large geographic areas, and it is intuitive to ask for data on large-scale climatic features. One example is the use of an index for the North Atlantic Oscillation (NAO) (Hurrell et al. 2003)—a measure of the sea surface pressure difference between the sub-polar and subtropical Atlantic—to understand plankton dynamics (Planque & Fromentin 1996).

However, large-scale climatic processes might equally well be important in terrestrial systems. For example, the effect of climate variation on the population ecology of red deer was shown by Post et al. (1997) using the NAO index—a contribution which brought the NAO into a variety of terrestrial studies (see also Hurrell 2003). Initially, the idea of using a large-scale climate proxy such as the NAO rather than local weather variables (such as precipitation and temperature) was met with much scepticism among terrestrial ecologists (Stenseth & Mysterud 2005). However, as evidence accumulated it became difficult to question the explanatory power of the NAO—also in terrestrial systems. The NAO later became a standard index to use in terrestrial studies around the Atlantic as the global nature of climatic systems and broad scale influences become clearer (Ottersen et al. 2001, Stenseth et al. 2002, Mysterud et al. 2003). This has facilitated a new way of looking at climate in terrestrial ecology. Again, through the mixing of expertise and insight from marine and terrestrial systems we have learned more than we otherwise would have.

This is merely one example, but it illustrates something quite typical of the scientific enterprise. Such discoveries happen seemingly by chance (sometimes over a cup of coffee), but more easily when scientists blend: meeting and working together across old-established territories. Creating platforms facilitating such interactions would certainly benefit ecology.

**Blending ecology through literature search strategies, or through collaboration?** How can marine and terrestrial ecology most efficiently be made to cross-fertilise each other? There seem to be 2 possible solutions: closer collaboration, and/or marine and terrestrial ecologists should start reading each others' papers. The latter is easy to say, but much more difficult to do. Not the least due to the enormous amount of ecological work carried out today, scientists have to develop search images when deciding which papers (and journals) to read. Few terrestrial ecologists read *Marine Ecology Progress Series*, and most of them, when skimming perhaps 100 titles and abstracts each week, will just skip those with the 'marine' word and rather read the papers closest to their own field of interest. This reinforces the communication barrier. At larger ecology conferences, there tend to be separate marine and terrestrial sessions — again reinforcing the difficulties in blending the two sectors. Seminal papers can thus easily be overlooked. For example, life history of large mammals seems surprisingly similar in marine and terrestrial ecosystems. Eberhardt (1977), with reference to marine mammals, identified that with increasing DD there is a predictable sequence of life history changes, first affecting juvenile survival and age at first reproduction, and later the survival of prime-aged individuals. This important principle was brought into terrestrial ecology more than 20 yr later (Gaillard et al. 2000), again sparking the original author to present the principle in a more general setting (Eberhardt 2002). This illustrates that both marine and terrestrial ecologists should also publish in general journals such as *Ecology Letters*, *Proceedings of the Royal Society of London Series B*, *Proceedings of the National Academy of Sciences (USA)*, *Ecology*, because there simply is a wider readership for these journals; but publishing in these journals also requires that they make their reports attractive to a general audience (e.g. with regard to the article's title and discussion). Review papers including both marine and terrestrial ecologists as authors should be encouraged. For instance, Ottersen et al. (2001) and Stenseth et al. (2002, 2003) deal with effects of large-scale climate variability on terrestrial as well as marine ecosystems. A different, but equally inclusive, approach was taken by Stenseth et al. (2004) in a book that incorporates the knowledge of freshwater and terrestrial ecologists in an attempt to describe the properties of North Atlantic marine ecosystems.

**Uniting ecologists in practice.** Collaboration in interdisciplinary teams across systems is an efficient way to obtain new knowledge. We suggest that within academic groupings such as the Centre for Ecological and Evolutionary Synthesis (CEES) in Oslo, scientists from different fields are blended together into what we

believe is a more potent brew—statisticians, freshwater, marine and terrestrial ecologists meet daily. Most of the work is and will continue to be separate, but approximately every 10th paper is a joint project across ecosystem borders. Once in a while, we apply for common funding. Even the most specialized terrestrial and marine ecologists have learned from such interactions—and we are surely becoming better ecologists than we otherwise would have been. Indeed, joint work on different systems may often offer unique opportunities to unravel questions you would not even ask for single systems. Clearly, all ecologists can learn from cross-sectoral collaboration.

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## Imbalances in the reporting and teaching of ecology from limnetic, oceanic and terrestrial eco-domains

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**Introduction.** Communication barriers between terrestrial and aquatic ecologists undoubtedly set back ecology, restricting its effectiveness as a discipline. Although such a barrier is assumed to exist (e.g. Steele 1991, 1995), the degree of interaction between scientists working on these 2 eco-domains has rarely been investigated (but see Irish & Norse 1996, Ormerod 2003). Thus, we assessed the relationships between terrestrial and aquatic ecologists by surveying the representation of research from the different ecological

domains, and the reporting and teaching of mainstream ecology in major journals and textbooks. In particular, we evaluated whether there is an imbalance in the representation of eco-domains: (1) in the editorial boards, and the number of articles published in mainstream general ecology journals; (2) in general ecological societies; (3) in the literature cited in general ecology textbooks; and (4) in terms of the number of scientists and level of activity associated with each eco-domain. We also investigated whether (5) the main ecological questions addressed by aquatic and terrestrial ecologists are different.

**Editorial boards of mainstream general ecology journals.** To assess for imbalances in the representation of eco-domains in the editorial structure of the general ecology journals, we surveyed the topical expertise (categorized as terrestrial, marine, and limnetic) of the editorial advisors of the following broad-coverage periodicals (as of May 2005): *Ecology*, *Oecologia*, *Ecology Letters*, and *Oikos*.

From a total of 255 editors, 198 (78%) were primarily involved in terrestrial ecology; this percentage was similar for all 4 journals surveyed, ranging from 70 to 83% (Fig. 3A). The representation of marine vs. limnetic ecologists was similar, 10.6 and 11.8% respectively.

We cannot resist offering a provocative metaphor: the predominance of terrestrial ecologists holding editorial positions in the key broad-coverage journals is akin to 80% of a country's newspapers being edited by people who are sympathetic towards one socio-political point of view: this leads to a closed/controlled flow of information and ideas.

**Terrestrial vs. aquatic articles published in mainstream general ecology journals.** We surveyed the subject matter of the articles published by these same journals during 2004. The articles were categorized as being terrestrial, marine, limnetic, or theoretical/methodological in focus. Of the 1020 articles published by all of these journals, 708 (69.4%) dealt with terrestrial ecology, and 9.9 and 10.6% focused on marine and limnetic issues, respectively (Fig. 3B). These percentages are remarkably similar to the subject area expertise of the editorial advisory boards (Fig. 3A). However, additional information would be required to establish a causal relationship between the two. For example, we would have to have an estimate of the total number of scientists working on each eco-domain (see below). Statistics on the submission and rejection rates of articles to the general ecology journals—by ecosystem type—would also be needed. It would also be necessary to establish criteria for determining whether submitted articles were of general interest to ecologists: we cannot imagine that this characterization could be made in a totally objective manner, but would be pleased to be proven wrong. Such informa-

\*The views expressed herein are my own and do not necessarily reflect the official position of The Institute of Marine Research.

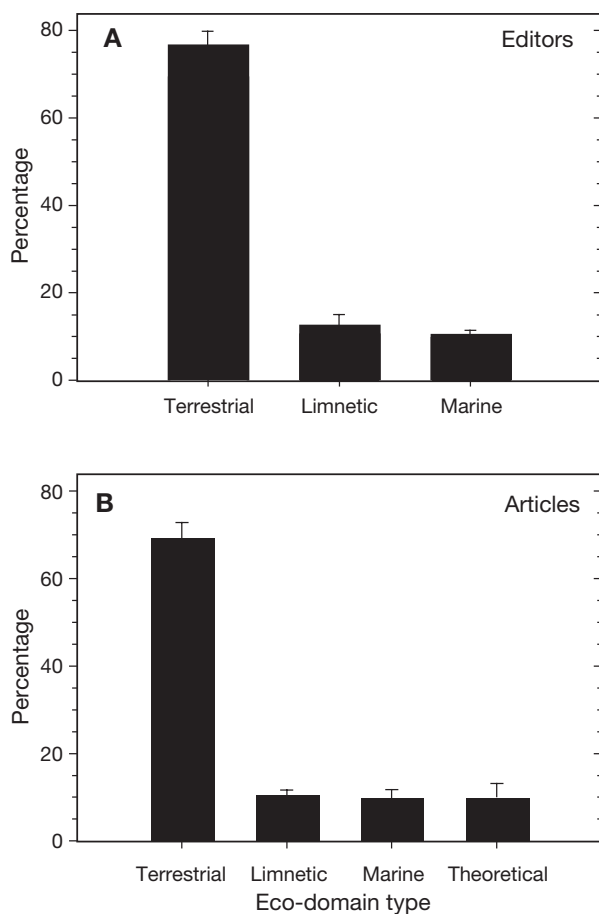


Fig. 3. (A) Expertise of editorial advisors in 4 general ecology journals, categorized by eco-domain type (in %, mean + SE); *Ecology* (editors), *Oecologia* (editorial board), *Ecology Letters* (editors), *Oikos* (subject editors, advisory panel and publication board). (B) Articles published in these journals classified by eco-domain type, plus the category 'theoretical'

tion would be difficult to obtain, and it may not even be retained by journals, although perhaps it should be.

#### Exchange of ideas and the education of ecologists.

As a first-order indicator of the penetration of aquatic ecology into the mainstream of ecology thinking (and its teaching), we examined the literature cited in the most recent general ecology textbooks (Smith & Smith 2002, Townsend et al. 2003, Odum & Barrett 2005). We categorized this literature as being: terrestrial, including general ecology journals, textbooks and books; aquatic, published in general ecology journals or books; or aquatic, published in aquatic journals or books. All references relating to wetlands, salt marshes, intertidal zones, and amphibians were included in the 'aquatic' category. Overall, the percentage of aquatic references varied from 11.5 to 18.2%. However, many of these articles (26.1 to 48.5%) appeared in general ecology journals or books. In addition, many of the

articles categorized as 'aquatic' were actually about wetlands, salt marshes, and the intertidal zone (which could reasonably be viewed as extensions of the terrestrial ecozone).

**Representation of eco-domains in ecological scholarly societies.** To determine whether the preceding statistics reflect the membership structure of general ecological societies, we canvassed the secretaries of the Ecological Society of America (ESA), British Ecological Society, International Association for Ecology (INTECOL), the French Ecological Society, the Ecological Society of Japan, and the Ecological Society of China, and requested the proportion of their members who characterized themselves as terrestrial vs. aquatic ecologists. We received a quantitative reply only from INTECOL and ESA. INTECOL gathers such information only from members that have joined (or renewed) online; these figures indicated that the representation is 80% terrestrial and 20% aquatic. Similarly, ESA currently has a total of 9264 members of which 874 (9.4%) are members of its Aquatic Section (Elizabeth Biggs, Director of Administration of ESA, pers. comm.), which is ESA's largest one (Nancy B. Grimm, President of ESA, pers. comm.).

One possible explanation for these society membership numbers is that there are far more terrestrial than aquatic ecologists. In order to assess this, we compared the total membership of the ESA with that of several American aquatic-oriented professional societies. The American Society of Limnology and Oceanography (ASLO) currently has some 4500 members of which about 25% identify themselves as working in ecology-related fields (Helen Schneider Lemay, Business Manager of ASLO, pers. comm.). The American Fisheries Society (AFS) has approximately 9000 members, 40 to 50% of whom are ecologists (Ghassan N. Rassam, Executive Director of AFS, pers. comm.). The North American Benthological Society has about 1500 members (Likens 2004), of which we will assume a conservative 25% to be ecologists. Thus, just these 3 American aquatic societies, together with ESA's Aquatic section, represent about 6500 to 7000 members who are ecologists. This figure is similar to the total ESA membership noted above. Although this is a very selective and proximate comparison, and there is surely at least some overlap amongst the memberships of these societies, it seems unlikely that there truly is an 80 to 90% preponderance of terrestrial vs. aquatic ecologists; the overall ratio is likely to be closer to 50:50.

**Number of papers/citations for terrestrial and aquatic journals.** During the period from 1981 to 2004, the annual number of articles published in 4 general ecology and 4 aquatic journals increased linearly (Fig. 4A). The slopes of the 2 regression lines did not differ significantly (ANCOVA,  $p > 0.05$ ) with ecotype, but the

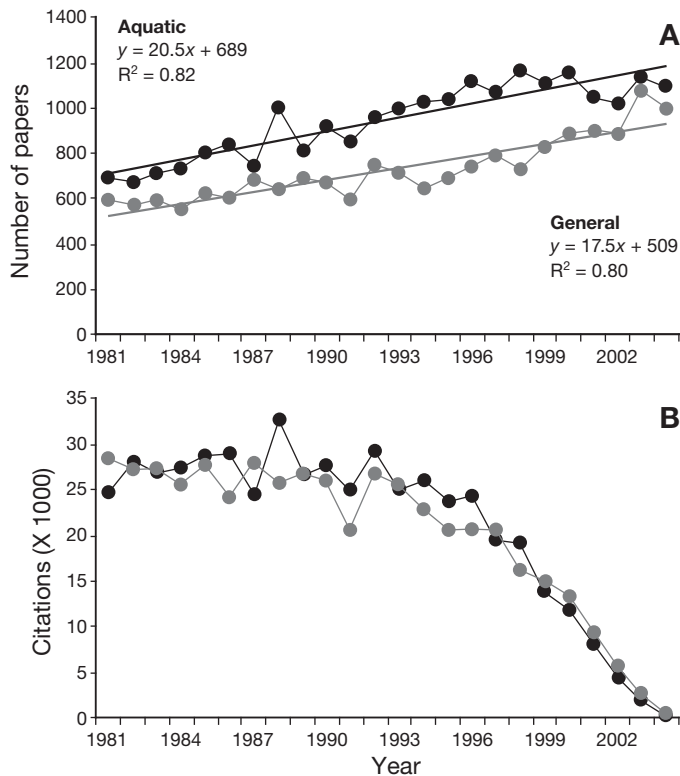


Fig. 4. Annual number of (A) articles and (B) cumulative citations for 4 general ecological journals (*Ecology*, *Oecologia*, *Ecology Letters*, and *Oikos*) (in grey) and 4 'aquatic' ecological journals (*Marine Ecology Progress Series*, *Journal of Experimental Marine Biology and Ecology*, *Canadian Journal of Fisheries and Aquatic Sciences*, and *Limnology and Oceanography*) (in black). The number for 1981, for example, equals the cumulative total number of citations to all articles published in 1981 during the period 1981 to 2004. Data commissioned from Thomson ISI, April 2005

intercept was higher for the aquatic journals (ANCOVA,  $p < 0.05$ ). Indeed, the mean total number of articles published in the 4 aquatic journals was significantly higher ( $t$ -test,  $p < 0.001$ ) than that published in the general ecology ones ( $945.5 \pm 32.7$  and  $727.9 \pm 28.3$  articles, respectively)—we point out here that the journal *Ecology Letters* is only published since 1999, i.e. during the 2nd half of the period analyzed. The annual cumulative number of citations followed the same pattern (Fig. 4B) and did not differ significantly ( $t$ -test,  $p = 0.72$ ) between general ecology and aquatic journals ( $21\,206 \pm 1901$  and  $20\,297 \pm 1715$  citations, respectively). The total number of articles published, and citations to these articles, for these 8 journals surveyed over the most recent 5 yr period for which data are available (2000 to 2004) are presented in Table 2. These numbers are fully consistent with the longer-term trends (Fig. 4).

While this is a selective and simplified sample, our results indicate that the imbalances between terrestrial

Table 2. Number of articles published in major general and aquatic ecology journals, and number of citations, during 2000 to 2004. Data commissioned from Thomson ISI, April 2005

| Journals  | Articles | Citations |
|---|----------|-----------|
| <b>Terrestrial</b>  |          |           |
| <i>Ecology</i>  | 1482     | 13012     |
| <i>Oecologia</i>  | 1455     | 8692      |
| <i>Oikos</i>  | 1247     | 6588      |
| <i>Ecology Letters</i>                                    | 561      | 3442      |
| Total   | 4745     | 31734     |
| <b>Marine</b>   |          |           |
| <i>Marine Ecology Progress Series</i>                     | 2360     | 11316     |
| <i>Canadian Journal of Fisheries and Aquatic Sciences</i> | 1043     | 5350      |
| <i>Limnology and Oceanography</i>                         | 1038     | 6746      |
| <i>Journal of Experimental Marine Biology and Ecology</i> | 1008     | 3322      |
| Total   | 5449     | 26734     |

and aquatic ecology so far reported are not based upon the numbers of ecologists nor the level of activity associated with the different eco-domains.

**Main ecological questions addressed by aquatic vs. terrestrial ecologists.** In order to assess whether the mainstream of activity and thought differs between terrestrial vs. aquatic ecologists, we extracted the 15 most cited articles (citation period: 1979 to May 2005; data from Thomson ISI) published in *Ecology* and *MEPS* (Table 3).

Many of the most highly cited articles in both journals referred to statistical–methodological topics. For *MEPS*, several highly cited articles were on microbial ecology, whereas others dealt with more spatially localized relationships between organisms and their environment. For *Ecology*, the subjects covered were generally more diverse, with many articles dealing with questions of large-scale spatial patterns in the distribution of organisms. In addition, 4 of the most highly cited articles in *Ecology* refer to the aquatic, notably freshwater, environment. The cumulative citations of the 15 articles were 8854 for *Ecology* and 7042 for *MEPS*. While we did not empirically evaluate it, our impression is that aquatic ecologists cite articles predominantly from the aquatic ecology journals and terrestrial ecologists predominantly from general ecology journals.

For both *Ecology* and *MEPS*, citations/article declined exponentially from the most highly to the least cited one (i.e. rank of article), with the rate of decline for *MEPS* (citations =  $1410 \times \text{rank}^{-0.68}$ ,  $r^2 = 0.97$ ,  $n = 15$ ,  $p < 0.05$ ) being steeper than that for *Ecology* (citations =  $1244 \times \text{rank}^{-0.44}$ ,  $r^2 = 0.95$ ,  $n = 15$ ,  $p < 0.05$ ). The latter might be an indication of the broader scope of the highly cited articles appearing in *Ecology*. This might be related to the longer history of terrestrial than marine ecology (i.e. research progresses from a de-



Table 3. The 15 most highly cited articles in *Ecology* and *Marine Ecology Progress Series* from 1979 to April 2005. Data commissioned from Thomson ISI, April 2005

| No.                                   | Author                     | Cites | Title   |
|---------------------------------------|----------------------------|-------|---|
| <b>Ecology</b>                        |                            |       |   |
| 1                                     | Terbraak (1986)            | 1260  | Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis  |
| 2                                     | Levin (1992)               | 1051  | The problem of pattern and scale in ecology   |
| 3                                     | Melillo et al. (1982)      | 752   | Nitrogen and lignin control of hardwood leaf litter decomposition dynamics  |
| 4                                     | Werner et al. (1983)       | 736   | An experimental test of the effects of predation risk on habitat use in fish  |
| 5                                     | Johnson (1980)             | 528   | The comparison of usage and availability measurements for evaluating resource preference  |
| 6                                     | Tilman (1994)              | 501   | Competition and biodiversity in spatially structured habitats   |
| 7                                     | Peterjohn & Correll (1984) | 489   | Nutrient dynamics in an agricultural watershed: observations on the role of a riparian forest   |
| 8                                     | Crowder & Cooper (1982)    | 487   | Habitat structural complexity and the interaction between bluegills and their prey  |
| 9                                     | Wilcove (1985)             | 474   | Nest predation in forest tracts and the decline of migratory songbirds  |
| 10                                    | Mittelbach (1981)          | 444   | Foraging efficiency and body size: a study of optimal diet and habitat use by bluegills   |
| 11                                    | Legendre (1993)            | 437   | Spatial autocorrelation—trouble or new paradigm?  |
| 12                                    | Borcard et al. (1992)      | 431   | Partialling out the spatial component of ecological variation   |
| 13                                    | Worton (1989)              | 425   | Kernel methods for estimating the utilization distribution in home-range studies  |
| 14                                    | Pastor et al. (1984)       | 421   | Above-ground production and N and P cycling along a nitrogen mineralization gradient on Blackhawk Island, Wisconsin   |
| 15                                    | Sousa (1979)               | 418   | Disturbance in marine intertidal boulder fields: the non-equilibrium maintenance of species diversity   |
| <b>Marine Ecology Progress Series</b> |                            |       |   |
| 1                                     | Azam et al. (1983)         | 1574  | The ecological role of water-column microbes in the sea   |
| 2                                     | Simon & Azam (1989)        | 695   | Protein content and protein synthesis rates of planktonic marine bacteria   |
| 3                                     | Field et al. (1982)        | 677   | A practical strategy for analysing multispecies distribution patterns   |
| 4                                     | Cole et al. (1988)         | 623   | Bacterial production in fresh and saltwater ecosystems: a cross-system overview   |
| 5                                     | Clarke & Green (1988)      | 430   | Statistical design and analysis for a biological effects study  |
| 6                                     | Wright et al. (1991)       | 424   | Improved HPLC method for the analysis of chlorophylls and carotenoids from marine phytoplankton   |
| 7                                     | Fenchel (1982a)            | 408   | Ecology of heterotrophic microflagellates. IV. Quantitative occurrence and importance as bacterial consumers  |
| 8                                     | Fenchel (1982b)            | 388   | Ecology of heterotrophic microflagellates. II. Bioenergetics and growth   |
| 9                                     | Clarke & Ainsworth (1993)  | 298   | A method of linking multivariate community structure to environmental variables   |
| 10                                    | Kjørboe et al. (1985)      | 291   | Bioenergetics of the planktonic copepod <i>Acartia tonsa</i> : relation between feeding, egg production and respiration, and composition of specific dynamic action |
| 11                                    | Børsheim & Bratbak (1987)  | 273   | Cell volume to cell carbon conversion factors for a bacterivorous <i>Monas</i> sp. enriched from seawater   |
| 12                                    | Highsmith (1982)           | 263   | Reproduction by fragmentation in corals   |
| 13                                    | Lewis & Smith (1983)       | 241   | A small volume, short-incubation-time method for measurement of photosynthesis as a function of incident irradiance   |
| 14                                    | Cloern (1982)              | 235   | Does the benthos control phytoplankton biomass in South San Francisco Bay?  |
| 15                                    | Fuhrman et al. (1989)      | 222   | Dominance of bacterial biomass in the Sargasso Sea and its ecological implications  |

scriptive and area–species specific approach to a large-scale and process-oriented approach, and becomes more diverse over time; see also Nobis & Wohlgemuth 2004).

**So, what is behind these numbers?** Our analyses demonstrated that there is a consistent 80 to 90% imbalance in the representation of the terrestrial ecorealm in the editorial advisory boards of general ecological journals (Fig. 3A), in the articles published in these journals (Fig. 3B), in the articles cited in general ecology textbooks, and in the membership of (at least some) ecological societies. In contrast, aquatic ecologists associate themselves with their own large soci-

eties, publish in their own journals, and are most probably cited largely by their aquatic colleagues (see below). It is intriguing to note that in soliciting contributions for this Theme Section most of those who declined the invitation were terrestrial ecologists.

Our results agree with those of Irish & Norse (1996) and Ormerod (2003), who consider only the 'conservation part' of ecology. Irish & Norse (1996) report that the aquatic articles that were published in the journal *Conservation Biology* (volumes 1 to 9(5)) made up only 14% (marine: 5%, freshwater: 9%) of the total, whereas the remaining ones were either terrestrial (67%) or general articles (19%). Similarly, Ormerod

(2003) notes that aquatic articles published in the *Journal of Applied Ecology* during 1983 to 2003 (which had the word 'restoration' in either the title or abstract) make up only 13% of the total (coastal: 4%; floodplains/wetlands: 4%; rivers: 3%; and lakes: 2%). These percentages are strikingly similar to those reported above.

Kochin & Levin (2003), stimulated by Irish & Norse (1996) and Ormerod (2003), looked at the impact of papers published in *Conservation Biology* by ecosystem category. They found that the average terrestrial article receives 2.56 more citations than the marine ones (18.2 and 7.1 citations, respectively) and conclude: 'Thus, not only were fewer articles being published about marine conservation, but those that were published appeared to have less impact than research on terrestrial habitats.' (Kochin & Levin 2003, p. 723).

These numbers demonstrate that there are significant—and counter-productive—barriers between terrestrial and aquatic ecologists. This is ironic when one considers that ecologists, in order to be effective, must communicate and interact with colleagues from *other* disciplines, as diverse as molecular biology, economics and environmental management. And they do so rather successfully, at least judging from the continuously new communication media arising to disseminate their work (e.g. journals such as *Molecular Ecology*, *Ecological Economics*, *Journal of Political Ecology*).

While it is difficult to identify the source of these imbalances, it is essential for ecologists to be aware of them and to reflect upon them, especially because existing barriers may be perpetuated as new generations of ecologists are trained by one or the other ecological school of thought. If ecology as a discipline is to flourish, it must address questions that are relevant across ecotypes and train ecologists who are willing, ready and able to do so.

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## Intertidal ecologists work in the ‘gap’ between marine and terrestrial ecology

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**Introduction.** When asked to contribute to this Theme Section, my first reaction was that there are few substantial differences between marine and terrestrial ecologists. This was, however, replaced by recollection of several recent ecological conferences where marine ecological topics were sequestered by organisers into separate sessions labelled ‘Marine Ecology’. For example, at the Ecological Society of Australia’s conference in Adelaide (Australia) in December 2004, there were many interesting sessions and themes, including such topics as dispersive organisms, demographic analysis and so forth. Then there were sessions labelled ‘Marine Ecology’, where entirely similar ecologists discussed topics such as dispersive organisms, demographic analysis and so forth. Subsequent conversation with colleagues in the USA and UK has convinced me that this is neither an isolated experience, nor a

national trait! So, there must indeed be divisions of the discipline because some meetings are divided on the basis of the medium in which the organisms live.

In passing, it is worth remembering that marine habitats and organisms are much older than terrestrial ones. Why terrestrial ecology is generally considered ‘general’ in comparison to marine ecology is odd. It probably relates to the historical blunder that caused our planet to be named ‘Earth’, despite the fact that the vast bulk of its surface and the even vaster bulk of its provision of 3-dimensional habitat is ‘sea’.

Of course, this notion of marine ecology being different is not a surprise when you consider the number of highly regarded international journals, such as *Marine Ecology Progress Series (MEPS)* and *Journal of Experimental Marine Biology and Ecology (JEMBE)*, which explicitly (and exclusively) cater to the whims and interests of marine ecologists. Their beginnings undoubtedly lie in their founders’ dissatisfaction with trying to publish valued contributions in the supposedly more general ecological journals. No doubt, Professor Harold Barnes (*JEMBE*) and Professor Otto Kinne (*MEPS*) became more than a little fed up with being told that some study is not of interest to terrestrial ecologists, so should not be published in a general ecological journal. I sympathise—I was told exactly the same thing by an editor of a major ecological journal during the period between being invited to write this and writing it.

Having to found new journals because there are perceptions of lack of interest in a sub-field is not new. Charles Elton became President of the British Ecological Society (BES) in 1932 and founded the *Journal of Animal Ecology* in 1933. The ‘parent’ journal (*Journal of Ecology, JE*) is now devoted to plant ecology and the BES was originally dominated by plant ecologists (McIntosh 1985). Perhaps *JE* was not satisfactorily receptive of contributions about animals? Anyway, the ecology in *JE* does not now routinely include animal ecology.

The founding of *MEPS* was to ‘update, deepen, widen and correct’ the available information, and was in ‘response to numerous marine ecologists from all over the world’ (Kinne 1979), but it was not made explicit why marine ecologists needed new and different venues. It is, I imagine, a potential gold mine of topics for research by social scientists to investigate why some editors think that terrestrial or marine ecologists are limited in what might be of interest to them. This assumes that, in fact, the ecologists were actually consulted!

Regardless of the reality or simply the perception of differences, it is important to recognise that there are equally large divisions within the 2 groups of marine and terrestrial ecologists. For example, in Australia,

most ecologists working on coral reefs do not attend the Australian Marine Science Association (AMSA) annual conferences. Fisheries biologists generally do not attend Ecological Society nor AMSA meetings and so on. Readers can identify their own national versions of these counterproductive divisions. It is a sad fact of life that, where marine ecology is isolated at more general meetings of ecologists, attendance at such meetings becomes a lower priority for marine ecologists.

As with many others, I consider myself to be an experimental ecologist. I use coastal, mostly intertidal, habitats to explore issues of interest about patterns, processes, methods, thinking and interpretation in ecology. It is important to attend conferences (and to read journals) about terrestrial and freshwater ecology to get insights and ideas. It is frustrating to see a lack of reciprocal interest in what marine ecologists do.

We intertidal ecologists occupy a strange no-man's land in any schism between terrestrial and marine sub-disciplines. During low tide, when most of us work in the field, the habitats are terrestrial. The animals and plants are subject to exactly the same environmental conditions as are their terrestrial counterparts. During high tide, the habitats are marine. The animals and plants are subject to the stresses, or are able to cash in on the advantages, provided by marine environmental conditions. As tides come in and go out, the habitats and organisms are often subject to major disturbances due to waves. These shifts between marine and terrestrial conditions cause major changes in biochemistry, physiology and behaviour, which have long been recognised as an important and fascinating area of research (e.g. Newell 1971, Moore & Seed 1985, Chelazzi & Vanini 1988).

So, intertidal ecologists have 1 foot in each habitat (despite some of us being accused of having 1 foot in our mouth). What insights does this schizophrenic view of habitat provide for perceptions of difference about ecology under different conditions? Here, I consider some things which may actually be different between the 2 major habitats.

**Structure of assemblages and some relevant processes.** It is commonplace in terrestrial and marine ecological studies to be concerned with multi-specific interactions and processes. We seem to have overcome the need to forget about the contexts of assemblages in which species live out their ecologies. So, we have moved past the situation in the early decades of ecological study where there was a schism between those who studied 'communities' because they were some type of super-organism (Clements 1905) and those who realized that ecology of assemblages would be best understood from knowledge of component species. The community/superorganism idea was all-pervasive for many years. It was so widely entrenched that Whittaker (1956) had to re-invent the term 'individual-

istic' to describe how species were distributed up a gradient of altitude (up a mountain).

Eventually the idea succumbed under the assaults of rationalists (Gleason 1926, Ramensky 1924 in Poniatovskaya 1961; see the historical account in McIntosh 1985).

Although studies of a 'community' rear their heads again (Underwood 1986) and in the guise of studies of an 'ecosystem' (Simberloff 1980), many ecologists study species in the context of the assemblages in which they are found.

Nevertheless, it is still very common to see terrestrial studies about use of resources by organisms of one type (say, birds or bees or beetles or ants), in isolation of other organisms requiring and using the same resources. Such taxocoenic studies (Pielou 1974) are not a problem, in that they test important hypotheses and are major contributions in their own right.

What is interesting from an intertidal ecological perspective is that investigations of use of resources of space—and, for organisms such as grazers, food supplies—are rarely interpretable without considering transphyletic interactions. For example, competition for food by grazing by small snails and limpets is strongly influenced by the simultaneous processes of occupancy of space by sessile animals. For example, where barnacles occupy a lot of the surface of rocks, grazing by limpets and snails is impeded (Dayton 1971, Connell 1972, Underwood 1979, Hawkins 1983, Underwood et al. 1983). The converse is also true—where grazers keep surfaces free from overgrowth by algae, they maintain empty habitat into which sessile space-occupiers like barnacles can recruit (e.g. Dayton 1971, Underwood 1985).

Such negative and positive interactions are, of course, widespread in ecology (see the review of indirect interactions by Wootton 1993). They are particularly in focus where food supplies for grazers are scattered in the same space that is needed by a diverse suite of sessile species (algae, barnacles, tubeworms, mussels, sponges, bryozoans). So, the provision of food equates to the provision of space, and grazers and sessile organisms need the same resource and interact fiercely to gain access to adequate supplies.

This phenomenon is not absent in terrestrial habitats, but there is no obvious terrestrial equivalent of sessile animals such as barnacles that occupy substantial amounts of space, thus eliminating portions of the supply of food for terrestrial grazers. Of course, there are sessile terrestrial species (e.g. leys, antlion larvae) and plenty of sessile plants, but there is no similarly widespread interaction between grazers and sessile animals as users of space. Note that the barnacles are pre-empting the resource—not modifying the habitat as ecosystem engineers (Jones et al. 1994).

It is worth noting that intertidal ecology also differs from the vast majority of marine ecology (by volume) that involves planktonic and nektonic—floating and swimming—organisms in the water-column. In the water-column, there are also no sessile space-occupying animals. It is a benthic phenomenon.

**Biodiversity.** In contrast to the above, intertidal habitats share a particular phenomenon with other marine habitats, such as the deep sea and the open ocean. This is the phyletic, rather than specific, diversity of organisms (see review by Gray 1997). Of the extant Phyla, 35 are marine (of which 14 are only marine) and only 11 are terrestrial (of which only 1 is non-marine). There are a further 14 freshwater Phyla, but none is endemic (Gray 1997). During the early (Precambrian) development of *baupläne*, marine habitats were obviously much more important than terrestrial habitats (Raup & Jablonski 1986). There has been no subsequent origin and radiation of Phyla (Valentine 1986). Many of the extant Phyla are confined to marine habitats (Gray 1997). Where there is evidence of extinct Phyla, such as in the Ediacaran fauna and fossils in the Burgess shale (Conway Morris 1979, Gloessner 1984), they were marine. There once were many more exclusively marine Phyla.

The opposite point of view is, of course, that some types of organisms are not *limited* to marine habitats. Rather, why bother to invade an inadequate terrestrial realm when everything is fine in the sea? Perhaps, invasion of land was by failures—only those organisms that could not make it in the sea had to develop a terrestrial mode of life!

We shall never know for certain why only some types of organisms occupy terrestrial habitats. Models and explanations are legion (Little 1990). If, as one biogeographic model has it, St. Patrick banished the snakes from Ireland (e.g. Delaney 2004), he obviously did a much more comprehensive job on, say, terrestrial cephalopods!

Given a marine–terrestrial difference in diversities of species and diversity of Phyla, it is interesting that there do not seem to be obvious processes that differ between the 2 realms. At the very least, examination of ecological literature reveals that, if there are processes that differ widely because of greater inter-specific diversity on land and greater inter-phyletic diversity in the sea, they are not being widely identified or discussed.

One reason that differences in phyletic or specific diversity do not matter has to do with resources, e.g. of food, space in which to live, light, or oxygen (i.e. the surrounding medium that transports it). If resources are in short supply, competition for resources will be important to organisms that overlap in their needs for them (Birch 1957). It makes no difference whether the

competitors are members of other species or other Phyla. There is no obvious reason why one or other type of diversity should lead to greater intensity of competitive interactions. More relevant are the responses of a suite of potentially competing organisms to the processes that lead to reductions in density (sizes, growth, reproduction, etc.). The relevant processes are those that determine whether or not there are sufficient competitors to prevent adequate supplies of resources for all organisms that need them. Such processes—notably diseases, harshness of environment (Andrewartha & Birch 1954), predators (e.g. Paine 1974), intraspecific competition (Darwin 1859) and supply-side issues (i.e. failures to recruit; Underwood & Denley 1984, Underwood & Keough 2001)—are apparently no more or less frequent or intense because of specific, as opposed to phyletic, diversity.

It is not clear how much the apparent lack of difference between terrestrial and marine ecological processes, despite the species–Phyla difference in biodiversity, is due to lack of relevant investigation.

**Spatial and temporal variability.** One area of large-scale (whole ‘system’) ecology that is purportedly different between terrestrial and marine realms is the nature of variance in time and, probably, space. There has been increasing interest in trying to understand and predict the consequences of variability, rather than ignoring it (Hurlbert 1984) or being baffled and frustrated by it. Cohen’s (1971) plaint that ecologists are beset with ‘physics-envy’ is valid. Physicists are beset with variance at the small scales where Heisenbergian uncertainty rules and at large, astronomical scales where small errors in numerous parameters can compound. In order to understand variability, it is essential to embrace, rather than to ignore it. It is therefore important to understand patterns of spatial and temporal variance in numbers of animals and plants.

One useful way of understanding variance at different scales is to use analogies of colour (e.g. the excellent synthesis by Schneider 1994). The ‘hue’ of a quantity is what happens when frequency of measurement changes (Fig. 5). ‘Red’ systems are those with greatest variability at small frequencies (long intervals); ‘blue’ are those with greatest variance at the large frequencies. ‘Green’ systems have a peak at some intermediate scale (Fig. 5) and ‘white’ systems show no change in variance with scale. Atmospheric temperature can be ‘white’, in that variation from year to year and from century to century (i.e. decreasing frequency) can be similar (e.g. Steele 1985). Populations which fluctuate in abundance more from season to season than from week to week or from year to year would have a ‘green’ spectrum of variability. Schneider (1985) suggested that natural examples of ‘blue’ spectra would

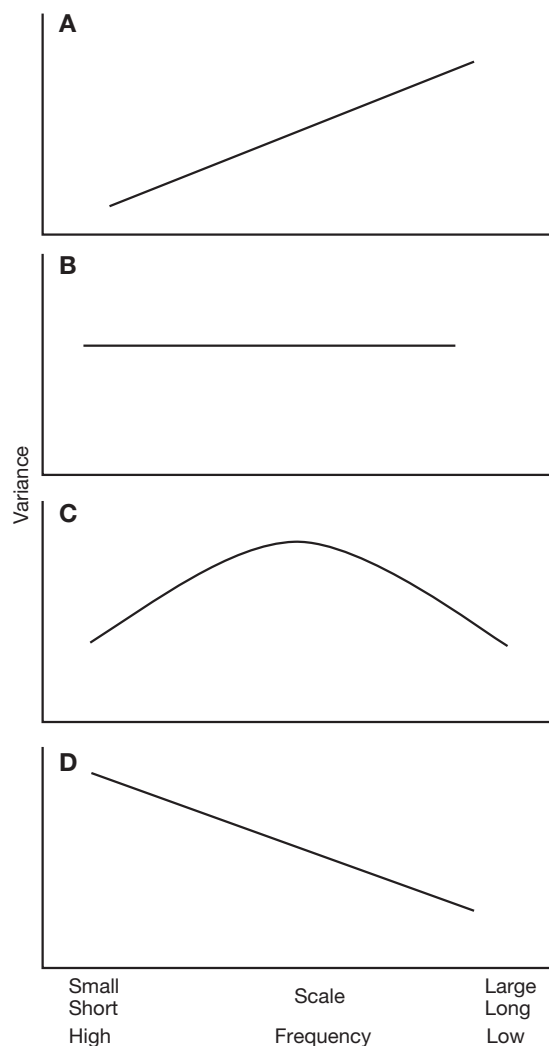


Fig. 5. Spectra of spatial or temporal variation, showing different patterns (or 'hues'): (A) red: variance increases with scale (i.e. with decreasing frequency); (B) white: variation is similar at all scales; (C) green: variation is greatest at intermediate scales; (D) blue: variance decreases as scale increases (after Schneider 1994)

be unusual. For example, numbers of organisms would have to fluctuate a lot in short time-periods (or differ a lot at small spatial distances), but over larger time-scales (or larger distances), changes (or differences) would dampen out.

There are serious difficulties in acquiring adequate ecological data over several temporal or spatial scales, and numerous methods for analysing and interpreting them (Schneider 1994, Horne & Schneider 1995, Underwood & Chapman 1996, Denny et al. 2004).

Nevertheless, despite these difficulties, Steele (1985) assembled data about temporal variance in temperature—a major physical variable in terrestrial and

marine habitats. The data show marked differences. Terrestrial systems show similar variance in atmospheric temperature over periods of 1 to 100 yr. In very marked contrast, temperatures in the deep ocean show increasing variance from hourly to yearly intervals of measurement. Records of sea level (which are linked to temperature) show increasing variance from hourly differences to 10-yearly differences (Steele 1985).

In this analysis, generalized terrestrial habitats show 'white' noise and marine habitats show 'red' noise. Short-term variability in oceanic temperatures is damped by the heat capacity of seawater (compared with air). Steele (1985) moved from this analysis to consider and predict how and why marine and terrestrial ecologies might have been maintained (and might have evolved) in different ways. Terrestrial systems therefore develop life-histories to cope with short-term variance, but these will also buffer against long-term fluctuations in environmental conditions. In marine habitats, according to Steele (1985), short-term fluctuations are small, so they elicit little adaptive response, whereas long-term fluctuations are large and marine populations will possibly show a stronger response to long-term changes than do their terrestrial counterparts.

Whatever the merits or difficulties of Steele's (1985) analyses, it is clear that the ecology of organisms in marine and terrestrial habitats will be very different. Direct comparison may prove futile because the inherent patterns of variability are not the same.

In passing, it is worth noting that several intertidal ecologists have found plenty of examples of 'blue' variance spectra in analyses of the spatial patterns of numbers of organisms (e.g. Bourget et al. 1994, Underwood & Chapman 1996). The variance in numbers per quadrat among quadrats a few metres apart is greater than the variability from site to site (10s m apart), shore to shore (100s m apart), etc. So, intertidal organisms get the blues in their spatial variation, largely because of small-scale processes that affect their recruitment, behaviour and interactions.

**Conclusion.** It is not realistic to attempt to be certain about differences in ecology between land and sea. It is probable that much of the perceived difference in ecologies is due to different ecologists. Underwood & Fairweather (1986) examined several examples of intertidal studies from temperate and tropical regions in different parts of the world. It was apparent that differences among regions, among types of organisms and among studies were very much influenced by the hypotheses, methodologies and interpretations chosen by the investigators. This is part of natural variation, but must influence any comparison of terrestrial and marine ecology. The variation amongst ecologies (and ecologists who work) in dif-

ferent marine habitats (deep sea to phytoplankton; sediments to rocky shores; tropical to polar) are probably at least as great as any difference between marine and terrestrial ecologies.

Nevertheless, there are noted differences that concern some areas of marine ecology compared with similar issues on land; 3 of these have been identified here: more focus on land on taxocoenes rather than trans-phyletic assemblages; specific versus phyletic patterns of biodiversity; different spectra of variation across time scales.

It is worth considering the consequences. For example, environmental impacts in marine habitats can often be detected at many scales of taxonomic resolution (Herman & Heip 1988, Olsgard et al. 1997, Chapman 1998). To what extent is this a function of non-specific biodiversity? Is the difference between phyletic and specific biodiversity an important one for managing conservation of coastal or other marine diversity (Gray 1997)? To what extent are different types of marine habitat (e.g. among intertidal habitats: mangroves, saltmarshes, rocky shores, sandy beaches) representative of marine systems? Do they really differ in meaningful ways from terrestrial systems? Are there really different patterns of temporal variance across similar scales, when measured relative to life-spans of the organisms (Frank 1981)? If there are, have we tested (and arrived at satisfactory conclusions about) hypotheses concerning stability and resilience of marine populations relative to terrestrial ones?

Are our perceptions of what is important on land versus in the sea due to any underlying real differences in processes? Or, are they simply related to the very real difference in visibility of organisms in the 2 realms? For example, ecologists who study terrestrial plants, birds or animals of many middling sizes can actually see (or hear) the organisms in nature, in groups, in real time and space. That is rarely true for ecologists studying fish or benthic marine invertebrates because of the opacity of the medium. Even when they can be seen, it is usually for very short periods over very small spatial scales.

Defining the contexts in which ecological studies fit is of obvious importance, whether or not marine and terrestrial ecologies are actually systematically different. Reflecting on differences—even if they are not real, or if real, intractable—at least gives one pause for thought about what might actually matter. Introspection, however self-indulgent, seems to be worthwhile. This paper will have made a contribution if it causes any reader to stop and think about something different.

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## Soils, freshwater and marine sediments: the need for integrative landscape science

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**Introduction.** Biodiversity and ecosystem processes are tightly coupled in freshwater, marine and terrestrial habitats. The soils and sediments in these habitats support an enormous richness of life, but are not often considered as interconnected subsystems. Academic training, professional societies, journals, and research programs have focused on terrestrial, freshwater, or marine ecosystems in isolation, rather than on their interconnections and parallel physical and chemical processes. Many ecosystem-oriented curricula studied by biologists emphasize that society is dependent upon the diverse biota that produce and process organic matter, whereas in the physical sciences curricula dealing with ecosystems focus more on geological and climatic drivers, rather than on biological relationships. Interdisciplinary ecosystem research remains a major challenge, because most ecology programs at universities that incorporate both biological and physical sciences are organized along traditional disciplinary approaches that focus on terrestrial, freshwater or marine ecosystems largely in isolation from the other domains. Some government agencies are beginning to connect biologists and physical scientists in team efforts to conduct ecosystem studies that not only transcend different areas of science, but that also cross domains. We believe that studies of this type will produce significant breakthroughs in our understanding of ecosystem processes.

Recent studies of biodiversity and ecosystem processes in soils and sediments are revealing new connections and parallels between terrestrial, freshwater and marine ecosystems that were previously unappreciated (Wall 2004). Evidence for the expansion of new ideas based on cross-disciplinary insights is beginning to appear in the scientific literature (e.g. Vanni et al. 2005), but examples are still uncommon. Aquatic and terrestrial ecologists seek to understand better the complex linkages among these interconnected below-surface species assemblages, because their loss can



affect multiple services, such as clean drinking water, soil fertility, and coastal ocean productivity. Moreover, destructive activities in one habitat often have dramatic consequences resulting from linkages between terrestrial, freshwater and coastal marine ecosystems. Sufficient funding is essential for long-term, comprehensive research that integrates large-scale biodiversity and ecosystem process data across soil and sediment environments, to provide information for managers and policy makers. However, such large grants are extremely rare. Without such research, our attempts to forecast impacts of disturbance across connected systems, such as those resulting from hurricanes and tsunamis, will continue to be primarily based on single disciplines, at small scales and over short terms. Management and restoration must aim at sustaining biodiversity in soil and sediment as an essential first step in sustaining ecosystem services to society.

Here, we discuss methodological and communication barriers between research on soils, and freshwater and marine sediments (referred to as the terrestrial, freshwater and marine domains, respectively), and how approaches in any one domain have influenced approaches in others. We assess perceived and actual similarities between domains in both ecosystem processes and the services they provide to humans, and address reasons for the differences in public policies and approaches to problem solving among these domains. We emphasize that changes in management and policy need to address large-scale, cross-domain threats and vulnerabilities, providing examples of some important linkages among domains. Finally, we present our assessment of priorities for future research and training, including collaborative, integrated initiatives.

**Communication barriers between domains.** Together, soil and sediment cover the majority of the Earth's surface and contain a vast diversity of unexplored life (see Table 4). Aquatic and terrestrial ecologists who study these ecosystems are united in their definition of ecology as a scientific discipline that is concerned with the relationships between organisms and their environment. However, lapses in communication among ecologists in different domains appear to develop during early disciplinary training, partially as a result of working in ecosystems under different abiotic and biotic constraints.

The ecosystems themselves are obviously distinct and require different methodologies. Soils and sediments appear initially to be similar, but in terms of structural complexity, soils generally have the greatest heterogeneity, while marine sediments have the least, with the possible exception of nearshore, coastal sediments. For terrestrial scientists, soil science becomes an important discipline in itself, often removed from disciplines dealing with freshwater lake and ocean sediments and frequently taught in colleges focused on agriculture and forestry.

Terrestrial ecology is also dominated by generations of plant-related scientists, as vascular plants play a central role in structuring soil. In contrast, plants are less important for freshwater and marine sediments, except in shallow areas. Biological differences between terrestrial plants and aquatic algae tend to further separate scientists in the different domains. Even in 'unifying' disciplines such as biogeochemistry, differences appear during graduate training, e.g. in the focus on the organic matter inputs that are the basis for most food webs. In soils, organic matter is supplied onto the surface (e.g. litterfall) and directly within the soil matrix (e.g. root turnover and exudation), whereas,

Table 4. Physical, chemical and biological properties of soils and sediments in the 3 domains (adapted from Wall 2004)

|  | Terrestrial  | Freshwater  | Marine                                       |
|--|--|---|--|
| <b>Parameters</b>                          |  |   |  |
| Global coverage ( $10^6$ km <sup>2</sup> ) | 120  | 2.5   | 350  |
| Carbon storage (Gt)                        | 1500   | 0.06  | 3800   |
| Organic content                            | High   | Low   | Low  |
| Oxygenation                                | Oxic to anoxic   | Oxic to anoxic  | Oxic to anoxic                               |
| Salinity                                   | Low  | Low to high   | High   |
| <b>Functional groups</b>                   |  |   |  |
| Primary producers                          | Plants, algae, microbes                                    | Macrophytes, algae  | Phytoplankton, plants, algae                 |
| Herbivores                                 | Invertebrate grazers (insects)                             | Invertebrate grazers (insects, crustaceans, molluscs)             | Suspension feeders, invertebrate grazers     |
| Predators                                  | Invertebrates (insects, arachnids, myriapods), vertebrates | Invertebrates (insects, crustaceans), vertebrates                 | Invertebrates (crustaceans), vertebrates     |
| Decomposers                                | Microbes   | Microbes, biofilm producers                                       | Microbes, meiofauna                          |
| Detritivores                               | Invertebrate litter transformers                           | Invertebrate litter transformers, deposit feeders, filter feeders | Invertebrate deposit feeders, filter feeders |

deep marine sediments receive the vast majority of their organic matter via deposition onto their surface, often from surface waters far above the seafloor. Freshwater sediments receive organic matter from a range of sources, from nearby riparian zones and from within the catchment basin (Wall Freckman et al. 1997, Covich et al. 2004). A further division between scientists studying the different domains is the spatial scale, which is large for marine systems, but can reach the microscale for freshwater sediments and soils (Lavelle et al. 2004). These differences in scale can develop into deep chasms early in academic careers.

Nevertheless, there are similarities that could bridge the communication gap and lead to greater integration of knowledge on ecosystems. While the species composition and abundance of organisms differ greatly among the terrestrial, freshwater, and marine domains, the major groups of organisms are similar. Bacteria are abundant in all domains, whereas fungi occur primarily in soils and in freshwater sediments. Estimates indicate the existence of as many as  $10^7$  bacterial genomes in 10 g of soil (Gans et al. 2005), illustrating the abundance and diversity of only a single taxonomic group in a single domain. Many of the same vertebrate and invertebrate Phyla occur in the 3 domains, although the greatest number of Phyla is present in marine sediments (Snelgrove 1999); the similarities and differences in biota among domains offer multiple avenues for discussion and comparison of organisms that share evolutionary lineages (Table 4). Scientists studying soils and sediments are unified on major issues concerning the organisms they study, such as the dearth of taxonomic information for invertebrates and microbes and the obstacles of sampling complex habitats. Indeed, only a small fraction of soil and sediment species are named and described, and the ecology of few of them has been elucidated (Brussaard et al. 1997, Snelgrove et al. 1997). Differences in habitat and biotic diversity between the 3 domains can also provide a motivation for dissolving the communication barriers that appear rigid throughout academic careers.

**Methodological barriers between domains.** Differences in the biological communities, in abiotic constraints, and in spatial scale among domains cause a requirement for training in different methodologies for sampling biotic components and measuring abiotic factors. Evaluating biodiversity is complicated in all of the domains by issues of scaling (local to regional), and by the fact that different sampling approaches and tools are needed for different sized organisms; in all domains this constraint leads to a schism in research, based on the size of the organisms studied. This constraint is being overcome by collaborative research within and among domains. Manipulative experiments to evaluate ecosystem services and biodiversity in all

of these domains are complicated by the feedback relationship between sediment/soil geochemistry and biota. Manipulating one without altering the other is extremely difficult. Moreover, many of the sophisticated tools that have been developed in recent years are also ecosystem specific, e.g. rhizotrons and canopy towers in the terrestrial domain. The need for ships in many aquatic sampling programs, and for submersibles to avoid blind sampling and to conduct replicated manipulative experiments, often characterizes large-scale marine and freshwater studies. In contrast, methodologies such as molecular approaches, statistical tools and stable isotope analyses are in general use, and they are beginning to demonstrate high levels of connectivity between domains (e.g. Koyama et al. 2005).

**Perception of ecosystem services provided by the domains.** Soil and sediment biota in the terrestrial, freshwater and marine domains perform numerous ecosystem services that benefit humans. Despite the many differences in physiochemical and biological properties between soil and sediment, these domains often provide similar or interconnected ecosystem services (Table 5). In each domain, for example, the biota mediate rates of decomposition and nutrient cycling, producing fertile soils and sediments and contributing to food production. Despite differences in community structure, soils and sediments contain functionally equivalent taxa that regulate these services. For instance, mixing by bioturbators (oligochaetes, molluscs and crustaceans in soil and freshwater sediments, and polychaetes, crustaceans, molluscs and echinoderms in marine sediments) is important in supporting services such as aeration, nutrient cycling, structure and maintenance of soil and sediment.

An integrated research approach is needed in order to understand and manage ecosystem services provided by the 3 domains (Table 5), yet human perceptions of these services often differ, and their values tend to be viewed in isolation. For example, the terrestrial domain is perceived as essential for food and fiber

Table 5. Major ecosystem services provided by soils and sediments are similar across the terrestrial and aquatic domains

| Ecosystem services   |
|--|
| Recreation habitat   |
| Decomposition of organic matter; major biogeochemical cycling    |
| Retention and delivery of nutrients to plants and algae          |
| Generation/renewal of soil/sediment structure and soil fertility |
| Cleansing of water, detoxification of wastes and pollutants      |
| Modification of hydrological cycles (floods, drought, erosion)   |
| Translocation of nutrients, particles and gases                  |
| Regulation of ecosystem responses to anthropogenic global change |
| Food production (for humans and livestock)                       |
| Landscape habitat heterogeneity                                  |

production, the freshwater domain as essential for recreation and provisioning of potable water, and the marine domain for food production, all of which are influenced directly or indirectly by soils and sediments (Wall 2004). Certainly, humans do harvest 99% of our food and fiber (including soil organisms such as mushrooms) from terrestrial systems (Pimm 2001), but marine fisheries typically provide most of the protein in coastal, developing countries. Each domain provides a range of other important services that are mediated by soils and/or sediments and their interactions are often coupled, but these linkages are often not well recognized. Environmental policy reflects human perceptions of weak linkages between domains, resulting in logging of watersheds with retention of only narrow riparian tree barriers to protect the freshwater domain. However, research across domains consistently shows their connectivity. For example, dust transport of biocontaminants from African soils are affecting Atlantic coral reefs (Garrison et al. 2003) and bioaccumulation of methyl mercury in insect larvae or adults in the freshwater domain can translate into a biocontamination in the terrestrial domain (Evers et al. 2005).

**Perception of the knowledge base between domains.** The perception of some ecologists is that terrestrial ecology is more 'advanced' than the study of the aquatic domains (Giller et al. 2004), but there are significant knowledge gaps that span all domains. Certainly, the scientific literature on the major producers in the terrestrial domain (plants), and on some of their main consumers (above-ground herbivorous vertebrates and insects), is much more extensive than that for their freshwater or marine counterparts. In contrast, literature on the diversity and function of the decomposer biota in the soil, freshwater and marine domain is similarly limited (Wall 2004). Ecological research in all 3 domains has focused on the megabiota (plants and vertebrates) (Clark & May 2002), leaving many questions regarding the roles of smaller organisms, which are typical of soils and sediments, largely unanswered. Since major research questions (e.g. food web theory, biodiversity and ecosystem function, and extent of carbon sequestration), where smaller organisms are thought to play a major role, are common to all 3 ecosystems, there are many opportunities for ecological research across the domains that address topics of considerable importance to humans. An indirect benefit of such research would be a reduction in the knowledge gap that exists between below-surface (i.e. soil and sediment) and above-surface research.

**Soil and sediment research, and scale.** Large-scale comparisons between the structure and function of terrestrial, aquatic and marine systems, such as the Hubbard Brook Ecosystem Study (Likens et al. 1970), are comparatively rare. This rarity reflects the scale of

most ecosystem research: it tends to be local and habitat specific (e.g. the ecology of tall grass prairie litter, riffles, or a single coastal embayment). Research across ecosystems at any scale is by nature extensive and expensive in research personnel, technology, data management, and requires large levels of funding and collaboration. Funding programs are often not structured in ways that allow cross-domain collaboration. For example, in the USA National Science Foundation, different panels are often responsible for funding projects in each of the domains. Most importantly, cross-ecosystem research requires vision, leadership and long-term commitment. This kind of research is increasingly being driven by the threats and vulnerabilities to ecosystem services across domains.

**Soil and sediment management in relation to threats.** Now and in the near future, soils and sediment face multiple threats that may impact upon the services they perform, not only within, but also across domains. These threats will affect the 3 domains at a range of scales (from local to global), and include factors such as agricultural and aquaculture intensification, urbanization, invasive species, rising atmospheric CO<sub>2</sub> concentrations and global warming (Table 6). Moreover, besides directly affecting the services of one domain, many of these threats indirectly impact upon the services provided by the other domains due to their interconnected nature. For instance, deforestation has potential consequences for freshwater and marine ecosystems (Ineson et al. 2004, and references therein). These linkages complicate decision making and planning, because the interactions are difficult to identify. An alarming example is the Mississippi River and Gulf of Mexico system, where land-based farming activities, in particular nutrient loading, have led to deterioration of large sections of the Mississippi River as a freshwater ecosystem. Moreover, hundreds of kilometers downstream, hypoxia zones in the Gulf of Mexico cover 1000s of km<sup>2</sup> and these zones exhibit complete loss of some key functions (Turner & Rabalais 2003). Another example of the connections between terrestrial, freshwater and marine domains is provided by Syvitski et al. (2005), who showed that humans have simultaneously enhanced sediment flux (i.e. erosion) from soils to rivers as a result of land use change (e.g. agricultural intensification, urbanization, and deforestation), increased sediment retention in freshwater systems, and reduced sediment flux to the coast as a result of damming. This highlights another key difference among domains. In terrestrial and even freshwater systems we are developing remediation programs that are sometimes quite successful. However, except for coastal wetlands, the only real management and remediation strategy that has been developed for marine sediments is to cease damaging activity (e.g.

Table 6. Vulnerability and threats to soils and sediments (modified from Wall et al. 2001)

|                      | Terrestrial  | Freshwater   | Marine  |
|----------------------|--|--|---|
| <b>Vulnerability</b> |  |  |   |
| Local scale          | Agricultural intensification, invasive species, pollution, habitat alteration, urbanization                        | Invasive species, land use change, habitat alteration, agricultural intensification, eutrophication, pollution | Invasive species, disease, coastal development, habitat alteration                                    |
| Regional scale       | Invasive species, pollution, habitat alteration, overexploitation  | Invasive species, land use change, habitat alteration, eutrophication, pollution, overexploitation             | Hydrological alteration, overfishing, habitat alteration, eutrophication, pollution, overexploitation |
| Global scale         | Climate change, rainfall and temperature patterns, UV radiation, circulation patterns, atmospheric CO <sub>2</sub> | Climate change, rainfall patterns, temperature patterns, atmospheric CO <sub>2</sub>                           | Climate change, rainfall and temperature patterns, UV radiation, circulation patterns                 |
| <b>Threats</b>       |  |  |   |
| Invasive species     | Imported soils, plants, wood, dust storms, dispersal events  | Ballast water, aquaculture, aquarium trade   | Ballast water, aquaculture  |
| Pollution            | Mining, agriculture, industrial waste  | Agriculture, sewage effluents, industrial waste, aquaculture   | Agriculture, sewage effluents, oil spills, industrial waste   |
| Habitat alteration   | Agriculture, logging, desertification, urbanization  | Fisheries, water extraction and diversion, dam building, channelization  | Ocean bottom trawling, fisheries, coastal reclamation, dredging                                       |
| Climate change       | Altered vegetation, climatic variability, erosion  | Severe drought, severe flooding, erosion   | Circulation changes, species compression  |

fishing, excess nutrient loading, and contamination) and to wait for improvements and possible recovery.

**Conclusion and recommendations.** Terrestrial, freshwater and marine habitats have traditionally been studied as distinct disciplines, largely as a result of predominantly within-discipline professional societies, journals, academic training, and research programs. Recent research showing the connectedness of below-surface systems, as well as human dependence on them, emphasizes the need for studies to integrate direct and indirect relationships across these complex systems. Although soils and sediments differ in physical and chemical properties and in many regulating variables, they are a source of mostly unexplored biodiversity that interacts to provide numerous ecosystem services to humans, and they are vulnerable to global change. Thus, it is important that below-surface biodiversity and ecosystem functioning not be overlooked in management and conservation (Wall et al. 2001). Moreover, due to the linkages among systems, degradation of one of them may have significant consequences for the others. Scientists, managers and policy-makers need a comprehensive understanding about how the biota in soils and sediments are linked and relate to numerous critical ecosystem functions. Below we highlight the topics that we feel need greater attention in future:

**(1) Training and research programs:** Scientists, universities, and research and education funding agen-

cies should be encouraged to target connections between ecosystems, rather than treating terrestrial and aquatic ecosystems independently of one another. To truly capture the large-scale (temporal and spatial) dynamics that operate between the terrestrial, freshwater and marine domains in a comprehensive fashion, financial commitments from funding agencies for collaborative projects will be necessary.

**(2) Linking ecology across the domains:** The majority of species that live in soil or sediment remain undescribed, and even the ecology of the described species is often poorly known. Although most species are specific to 1 domain, there are functionally equivalent species in soils and sediments. Thus, joint conferences by professional organizations, such as the Soil Ecology Society and the American Society for Limnology and Oceanography, would provide a good opportunity for eliminating or lowering some of the barriers between research in the 3 domains. This integration has occurred, albeit in a limited fashion, in relation to ecosystem processes at Ecological Society of America conferences; however, community structure and species effects are still sometimes neglected when the focus is on ecosystems. The recent American Association for the Advancement of Science symposium on sustaining biodiversity and ecosystem services in soils and sediments provides an excellent example of how research findings in the 3 domains can be combined.

**(3) Cross-domain experiments:** It is apparent that the hydrological, biogeochemical and biodiversity connections that occur across the below-surface domains are also integral to the functioning of the above-surface systems. Experiments addressing these linkages across multiple scales are critically needed for informed sustainable management. As with other areas of ecology, the advancement of technologies, from molecular to large-scale global analyses, for each separate domain must be fully employed in multi-site, cross-domain global experiments, if we are to know how the earth system is changing.

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