What is the relationship between productivity and animal species richness? A critical review and meta-analysis

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ATTESTATION OF AUTHORSHIP

I hereby declare that this submission is my own work and that, to the best of my knowledge and belief, it contains no material previously published or written by another person (except where explicitly defined in the acknowledgements), nor material which to a substantial extent has been submitted for the award of any other degree or diploma of a university or other institution of higher learning.

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ACKNOWLEDGEMENTS

ABSTRACT

Understanding spatial patterns of species diversity is a central goal in ecology. Species richness has often been shown to correlate strongly with ambient energy, available energy or primary productivity. Theories that invoke energy as an underlying factor driving species richness have received much attention. However, the relationship between species richness and energy is not always linear and can vary with scale. Here I present the results of a meta-analysis of published animal–productivity species richness relationships (A–PSRRs). Initially, 387 separate cases from 267 published studies were identified as potential tests of the A–PSRR. After critically assessing each study, 141 separate cases were accepted as robust tests of the A–PSRR, of which 112 had data available for re-analysis. Positive A–PSRRs were found to predominate at all scales (geographical extents and grains), in terrestrial and freshwater ecosystems and homeo- and poikilotherms. Marine ecosystems contrasted with the general patterns with unimodal relationships being the most common form of the A–PSRR.

The results reported in the present study contrast with predictions that the true form of PSRR is unimodal, and with a previous review that found that no particular form of the A–PSRR was dominant. Importantly, the previous review has been criticised for its treatment of scale, surrogates for measuring productivity, relaxed criteria for including studies in the analyses and statistical methods. The present study addresses these issues and finds the contrast with the previous review of the A–PSRR is related largely to the statistical methods used for classifying relationships and, to a lesser degree, the use of strict study selection criteria in the present study. The predominance of positive A–PSRRs found in the present study compares with a recent review of the plant–PSRR which also reported that positive relationships predominate after addressing the issues of scale, surrogates, selection criteria and statistical methods.

The results of the plant–PSRR and A–PSRR are consistent with evidence that a number of taxa (poikilotherms and homeotherms) have faster rates of molecular evolution in warmer and more productive environments.

1. INTRODUCTION

1.1 Patterns of diversity

Biological diversity is non-randomly distributed across the Earth. Notable patterns are the decline is species richness with increasing latitude, altitude and decreasing ocean depth. The gradient of species richness with latitude is an ubiquitous pattern across a broad range of taxa, scales and habitats, with few exceptions (Hillebrand, 2004). However, latitude, altitude or depth themselves cannot be the determinants of diversity and the underlying mechanisms driving or constraining species richness need to be identified (Hawkins & Diniz-Filho, 2004). The change in prominent environmental variables is shared across latitude, altitude and depth, and this might provide insight into the potential mechanisms involved in determining diversity. Temperature declines along all three gradients suggesting that temperature plays a role in diversity patterns with higher temperatures driving diversity, colder temperatures constraining diversity or a combination of the two. Alexander von Humboldt (1808) recognised the potential role of climate over two centuries ago when he first described the latitudinal diversity gradient (LDG) suggesting that tropical regions have higher diversity because higher latitudes are cold and can be considered harsh. However, some of the hottest places on Earth are deserts, which are often depauperate of life suggesting that temperature cannot be the sole determinant of species richness. Biologically available energy on the other hand correlates with species richness more generally and the interaction between water and energy, either directly or indirectly, "is a likely candidate for a short list of explanations" (Hawkins, Field et al., 2003, p. 3106).

1.2. Energy and species richness

Available energy or productivity has long been recognised to relate strongly with species richness across broad scales (Evans, Warren, & Gaston, 2005; Hawkins, Field et al., 2003). The species–energy relationship holds for a range of taxa from local to global scales (Abramsky & Rosenzweig, 1984; Brown, 1973; Currie, 1991; Hawkins, Porter, & Diniz-Filho, 2003) pointing to energy as a prominent factor in determining species richness. However, two issues can be identified with the species–energy relationship: (1) the relationship between species richness is not always linear, and can vary with scale (Chase & Leibold, 2002; Currie et al., 2004; Gillman & Wright, 2006; Mittelbach et al., 2001; Waide et al., 1999); and (2) a relationship does not prove causality; a mechanistic driver related to energy needs to be determined.

Hutchinson (1959) first proposed the idea that available energy/productivity controls spatial patterns of diversity through trophic cascading suggesting that more energy can support longer food chains and thus more species. However, the form of the relationship between species richness and productivity is not always positive, and some argue that a unimodal, hump-shaped relationship (Figure 1) is the 'true' (Rosenzweig, 1992) or 'ubiquitous' (Huston & DeAngelis, 1994) form of the PSRR. The form of the productivity–species richness relationship (PSRR) is scale dependent, with unimodal relationships being more common at small scales, and positive relationships predominating across larger scales (Chase & Leibold, 2002). Scale dependency indicates that the mechanisms driving species richness patterns at different scales may not be the same.

A number of reviews of the PSRR have presented contrasting results. Gillman and Wright (2006) find that positive relationships predominate for plants at all but the smallest scales while Mittelbach et al. (2001) find that the

relationship is commonly unimodal and scale dependent. In order to understand

the underlying mechanisms shaping the PSRR, it is important to first determine

what the predominant form is and whether the form is indeed dictated by scale.

Below, I discuss the reviews of the PSRR, highlighting their strengths and

shortcomings. The results of the aforementioned reviews are then placed in

context of theories that might explain the observed relationships.
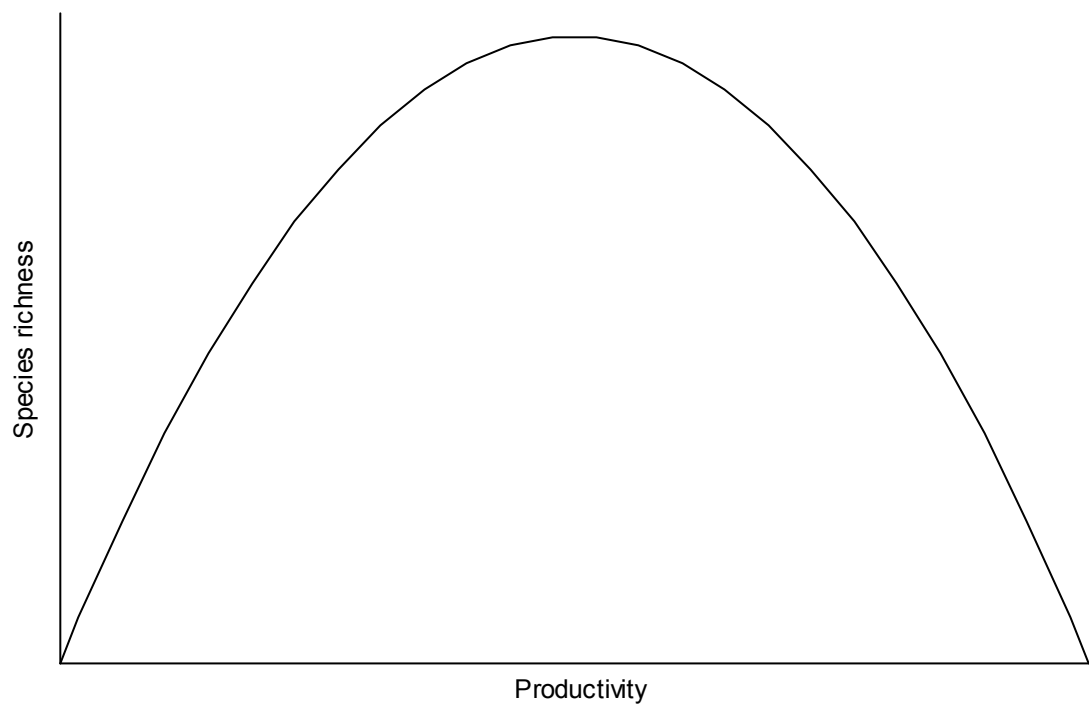
Figure 1. The hypothesised unimodal or hump-shaped relationship between productivity and species richness.

1.3 Reviews of the PSRR

Reviews and meta-analyses of the PSRR have contrasted with the predictions of a unimodal relationship made by Rosenzweig (1992) and Huston and DeAngelis (1994), instead reporting that the PSRR is not always unimodal, but can be variable and scale dependent (Gillman & Wright, 2006; Mittelbach et al., 2001; Waide et al., 1999). However, aside from showing that the form of the PSRR is variable, these reviews share little similarity in their conclusions about which pattern predominates. The earliest of these reviews was a narrative review and can be viewed as less formal than later reviews (Waide et al., 1999). The second review (Mittelbach et al., 2001) was largely undertaken by the same working group as Waide et al. (1999) following more formal protocols including a re-analysis of raw data where possible. The work of Mittelbach et al. (2001) focussed on plants and animals in terrestrial and aquatic (marine and freshwater) ecosystems. Their results suggested that unimodal relationships were the most common form of the plant–PSRR at all except the largest scale scales—positive and unimodal relationships were equally common at the largest geographic extent. For animals, no single form predominated, except at the largest scale where unimodal relationships were most common.

A subsequent comment and critical analysis of Mittelbach et al. (2001) by Whittaker and Heegaard (2003) raised some important issues (discussed below) regarding the inclusion of studies that were not robust tests of the PSRR, and that potentially contributed to a disproportionate number of unimodal relationships in the dataset. The critical analysis of Mittelbach et al. (2001) prompted a complete reassessment of the PSRR of terrestrial plants (Gillman & Wright, 2006). The results presented by Gillman and Wright (2006) contrasted with those of Mittelbach et al. (2001), with positive relationships being predominant across the whole dataset, at

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coarse and fine grains and, at continental-to-global and regional geographic extents (see *1.4.1 Scale* below). The review of Mittelbach et al. (2001), the comment by Whittaker and Heegaard (2003) and the re-analysis by Gillman and Wright (2006) are discussed in detail below. An additional study by Pärtel, Laanisto and Zobel (2007) is also discussed in light of a recent forum in *Ecology* on meta-analyses of the PSRR; all three reviews, including the critical analysis by Whittaker and Heegaard (2003) were published in *Ecology*.

1.4. Critical analysis of PSRR reviews

Literature synthesis is a useful tool for addressing common questions in a field of interest. Furthermore, meta-analyses allow the combination of numerous studies to test the generality of a phenomenon. However, meta-analyses are sensitive to the methods employed for selecting studies for inclusion in the final analysis (Cooper, Hedges, & Valentine, 2009; Gurevitch & Hedges, 2001; Whittaker, 2010b). These methods for assembling and analysing studies can therefore lead to erroneous conclusions. The reviews by Mittelbach et al. (2001) and Pärtel et al. (2007) were criticised by Whittaker and Heegaard (2003) and Whittaker (2010b) respectively on three main issues; (1) their treatment of scale; (2) their use of productivity surrogates; and (3) the methods used for classifying the form of the PSRR. These issues are discussed below.

1.4.1. Scale

Scale consists of multiple components, and the processes that act at different scales, and the different aspects of scale (Table 1) can influence the form of species richness relationships (Whittaker, Willis, & Field, 2001; Willis & Whittaker, 2002). Studies that

have used the same data, but aggregated it at different grains have found that the form of the PSRR is positive at coarse grains, and unimodal at fine grains (Braschler et al., 2004; Chase & Leibold, 2002). Similarly, the PSRR is predicted to be unimodal at small geographical extents (Rosenzweig & Abramsky, 1993) and positive across macro-scales (Currie, 1991; Wright, Currie, & Maurer, 1993).

Mittelbach et al. (2001) only considered one aspect of scale (extent), and ignored another important aspect of scale (grain). Pärtel et al. (2007) made no distinction between studies of different extents or grains. In contrast to the predictions about extent, Mittelbach et al. (2001) reported unimodal relationships as predominant at all but the largest geographic extent where positive and unimodal relationships were equally common. On the other hand, after categorising studies by geographic extent and grain, Gillman and Wright (2006) found that positive terrestrial plant–PSRR relationships were predominant in both coarse and fine grain studies, and all but the smallest extent.

1.4.2 Use of productivity surrogates

Productivity is a measure of biomass accumulation per unit area per unit time (e.g. $g/m^2/yr$). However, measuring biomass accumulation is often difficult and/or impractical. For example, forests consist of large slow-growing individuals. Therefore, removing the current biomass and measuring the rate of new biomass accumulation would be time consuming, not to mention the obvious damage such methods would have on the area of interest. Biomass turnover can however be measured using other methods such as leaf litter accumulation (Keeling & Phillips, 2007). However, across broad scales this method is labour intensive. Ecologists therefore rely on variables to represent productivity and these surrogates can vary depending on the ecosystem being studied. The surrogates commonly used in terrestrial ecosystems are rainfall and actual

evapotranspiration (AET), in freshwater ecosystems they are nutrient and chlorophyll *a*

concentrations, and in marine systems depth is most common. Importantly, however,

some surrogates do not always have a linear relationship with productivity. Mittelbach

et al. (2001) and Pärtel et al. (2007) commonly considered rainfall and biomass as

surrogates for productivity, yet neither has a uniformly positive relationship with

productivity. Additionally, Pärtel et al. (2007) used the "number of soil resources" (p.

1093) to represent productivity. These three surrogates and their pitfalls are discussed

below for general applicability.

Table 1. The different aspects of scale, and the putative processes influencing species richness. Adapted from Whittaker at al. (2001) and Willis and Whittaker (2002).

Scale	Definition
Extent	The total geographical area covered by a study or the greatest distance between sites within a study.
Grain	The size of the sampling unit used for comparisons. It may take the form of transects, quadrats or grid squares. It is important for grain to held constant within studies to allow for meaningful comparisons and, for the grain size to be appropriate for the target taxa. For example, Evans et al. (2005) suggest grain should scale with body size given that foraging range tends to increase with body size. Thus fine scale for one taxon might be coarse scale for another (e.g. birds and ants).
Local-to-landscape extent	Within or between communities over a small area containing a single or few habitat types (i.e. < 200km). Most likely to be influenced by species interactions, disturbance and dispersal over short time periods ~1-1000 years.
Regional extent	Between communities across large geographical areas but smaller than whole continents such as a country covering multiple ecosystem types (i.e. 200–4000km). Influenced by large scale climatic conditions or area over the last 10,000 years.
Continental-to-global extent	Across entire continents or the whole Earth spanning multiple biomes or bioregions (i.e. >4000km). Influenced by speciation, extinction, glaciations and continental drift.
Fine grain	Point or alpha diversity, reflecting within community diversity and local interactions.
Coarse grain	Larger than the above capturing more of the species pool in a single sampling unit reflecting beta-gamma diversity, or cross community diversity.

(i) Rainfall

In arid regions, rainfall is a good surrogate for productivity because water is the limiting factor for growth. In mesic to wet regions water is not a limiting factor and as rainfall increases productivity can decline (Kay, Madden, Van Schaik, & Higdon, 1997; Keeling & Phillips, 2007) indicating that rainfall cannot be used as a surrogate for productivity in these environments. Rainfall can also be confounded by elevation. As elevation increases, cloud cover and temperature generally decrease. Under these conditions energy is the limiting factor for growth (Scurlock & Olson, 2002), and productivity can decline with increasing rainfall and elevation making rainfall an unsuitable proxy for productivity (Kay et al., 1997; Whittaker & Heegaard, 2003). Hence, rainfall only approximates productivity in certain circumstances and should be applied with caution.

Whittaker and Heegaard (2003) highlight a study Mittelbach et al. (2001) classified as a unimodal plant–PSRR using rainfall as a surrogate. The study in question (Kay et al., 1997) reported a non-linear, unimodal relationship between rainfall and productivity in the same habitat type. Thus, rather than being a unimodal response to productivity, there is most likely an underlying positive plant–PSRR (Whittaker & Heegaard, 2003). Using annual rainfall as a surrogate, Pärtel et al. (2007) included four studies in their analysis from regions with low mean annual temperatures (< 10°C). Although a cut-off of ten degrees Celsius is somewhat arbitrary, it is used to demonstrate the point that the use of rainfall as a surrogate for productivity is inappropriate in cold climates. Plant activity is dependent on an interaction between water and energy (O'Brien, 1993). At high levels of rainfall, water is no longer a limiting factor for plant growth and energy becomes more important (Scurlock & Olson, 2002).

An interesting example is the study by Phillips et al. (1994). Mittelbach et al. (2001) and Pärtel et al. (2007) used rainfall and species richness data from Phillips et al. (1994). Pärtel et al. (2007) classified it as positive, and Mittelbach et al. (2001) classified it as unimodal. The positive relationship reported by Pärtel et al. (2007) using rainfall is difficult to understand given that both the correlation reported by Phillips et al. (1994) ($r = 0.33$, $P = 0.103$), and a re-analysis using OLS regression indicates that the relationship is non-significant (lin., $R^2 = 11.1\%$, $P = 0.103$; quad. model, $R^2 = 21.2\%$, model, $P = 0.072$, quad. term, $P = 0.107$). Whittaker and Heegaard (2003) analysed Phillips et al. (1994) in their comment and deemed it inadmissible on the basis that the range of rainfall in the study reached 4000mm/yr. At ~4000mm/yr productivity begins to level off, or decline, and less of the variability is explained by rainfall (Kay et al., 1997; Scurlock & Olson, 2002). Furthermore, Gillman and Wright (2006) concluded that the rainfall data in Phillips et al. (1994) were confounded by elevation and latitude. Importantly however, Gillman and Wright (2006) re-analysed the data using the tree turnover metric reported by Phillips et al. (1994), a more direct measure of productivity, and found a positive tree–PSRR.

(ii) Biomass

Biomass growth/turnover provides a good measure of productivity in tropical and temperate forests (Keeling & Phillips, 2007). However, in boreal forests, fire modifies the relationship between biomass turnover and productivity (Keeling & Phillips, 2007). Disturbances such as herbivory are also likely to influence the relationship between biomass accumulation and productivity and can counteract other drivers of productivity (McNaughton, 1985; McNaughton, Banyikwa, & McNaughton, 1998). Moreover, using biomass can only be acceptable as a surrogate for productivity there is little variation in

habitat type and size of individuals because a few large individuals can contribute disproportionately to biomass. Standing biomass on the other hand, does not necessarily equate to the productivity of a habitat and if generation times differ between habitats care should be taken in using it as a surrogate for productivity (Gillman & Wright, 2006). Temperate forests can have higher biomass than tropical forests, but tropical forests are more productive because the rate of biomass turnover is greater (Keeling & Phillips, 2007). Furthermore, Keeling and Phillips (2007) reported that at high levels of productivity, biomass levels off with increasing productivity, or even declines due to lower wood densities in tropical forests. Thus, given that biomass explains less variation in plant species richness, and often has a non- linear relationship with productivity, using standing biomass as a surrogate for productivity is inappropriate. Pärtel et al. (2007) used standing biomass more often (33.1% of studies) than any of the other surrogates they considered (precipitation, 29.4%; biomass growth, 14.7%; 'soil resources', 12.9%; other, 9.8%). Using standing biomass as a surrogate, Pärtel et al. (2007) reported unimodal and non-significant relationships to occur in similar frequencies (40.7 and 37.0% respectively). Mittelbach et al. (2001) included a similar proportion of studies with biomass as a surrogate (32.1%) finding that unimodal relationships were predominant (51.9%).

(iii) Soil resources

The number, or amount, of 'soil resources' cannot be applied as a surrogate for productivity in a general sense. Plant productivity is complex and plant activity relies on water and energy input in addition to nutrients (O'Brien, 1993). Therefore, if sites differ in their energy and rainfall regimes, the influence of soil nutrients might be confounded. Huston and Wolverton (2009) argue that the concentration of exchangeable bases (K,

Ca, Mg, Na) and, nitrogen and phosphorous in the soil have high importance for productivity. The above suggestion reveals, an apparent 'paradox' because soil exchangeable base concentration increases with latitude; this is contrary to the view that productivity decreases with latitude (Keeling & Phillips, 2007). However, an alternative interpretation is possible. Low soil nutrient concentrations in tropical regions are due to rapid biomass turnover, and the majority of nutrients are locked in plants rather than in the soil as in higher latitudes. Huston and Wolverton (2009) argue that ecologically relevant productivity is higher in temperate than tropical zones. However, their hypothesis requires a systematic global sampling effort to provide support, which as of yet has not occurred.

In their study, Pärtel et al. (2007) provide no explicit description of how they classified 'soil resources' other than 'the amount of different soil nutrients.' Pärtel et al. (2007) also did not state whether they considered terrestrial or aquatic environments, or both. Based on the classification of 'soil resources', it might be assumed that they focused on the terrestrial environments. However, an examination of their online appendix reveals a study that examined the influence of nitrogen and phosphorous on algal species richness in freshwater ponds (Leibold, 1999). Pärtel et al. (2007) conclude a hump-shaped relationship, but it is unclear whether they based their conclusions on the nitrogen or phosphorous data. Importantly, Leibold (1999) concludes that the relationships were "decreasing or (more likely) humped", but regardless of whether the relationships were unimodal or negative, Pärtel et al. (2007) would have classified the relationship as unimodal (see *1.4.3 Statistical issues* for discussion on reclassification of negative relationships). Whittaker (2010b) addresses two studies included in Pärtel et al. (2007) in which 'soil resources' are used as a surrogate for productivity. Pärtel et al. (2007) classified both studies as unimodal. One of the studies (Monk, 1965) (also used by Mittelbach et al. (2001) and classified as negative) used a measure of soil moisture.

High soil moisture leads to water logging and Monk (1965) suggests that the saturation of the soil limits diversity. The other study Whittaker (2010b) addresses (Stevens, Dise, Mountford, & Gowing, 2004) was included only by Pärtel et al. (2007). Pärtel et al. (2007) classified the relationship as unimodal (reclassified from negative) using nitrogen concentration as a surrogate for productivity. However, Whittaker (2010b) identified that nitrogen concentration correlated with high acidity and climatic variables were not controlled for: both of these factors may have confounded the influence of nitrogen.

1.4.3 Statistical issues

Using either data obtained from authors, or digitised figures, Mittelbach et al (2001) determined the form of the PSRR using both ordinary least squares (OLS) regression and generalised linear model (GLM) regression (with a Poisson distribution and a log-link function). In their final analyses, Mittelbach et al. (2001) presented the results from the GLM regressions (using a 10% significance level) in preference to the OLS results. Whittaker and Heegaard (2003) however, identified two issues with this approach. The first issue relates to the level of significance. Mittelbach et al. (2001) argue that using a 10% level of significance is suitable because it is liberal in detecting a pattern. However, using this level of significance is likely to bias toward complex relationships (i.e. quadratic hump- and u-shapes) and is an atypical practice for species richness patterns (Whittaker & Heegaard, 2003). The second issue raised relates to the use of GLM regression and the assumption of a Poisson distribution. If a Poisson distribution is assumed the variance must equal the mean. However, this is rarely the case in ecological data; variances are frequently higher than means, resulting in overdispersion. While it is possible to correct for overdispersion in GLM regression if the degree of

overdispersion is small, Mittelbach et al. (2001) made no correction for overdispersion. Furthermore, species richness data is less likely to violate assumptions of normality and symmetry of errors required by OLS regression, than it is the assumption of a Poisson distribution (Gillman & Wright, 2006). Importantly, by running simulations Whittaker and Heegaard (2003) demonstrated that failing to correct for overdispersion can bias towards accepting unimodal relationships.

Pärtel et al. (2007) provide no methods for how studies were classified. Whether they relied on the classification by the primary authors, Mittelbach et al. (2001) or Gillman and Wright (2006) is unclear and/or varies (Whittaker, 2010b). Unlike other studies on the PSRR, Pärtel et al. (2007) considered only positive, unimodal and non-significant relationship. Negative relationships were classified as unimodal, and u-shaped relationships were classified as non-significant. Pärtel et al. (2007) argued that no life can exist in zero productivity and all PSRRs must begin from an origin of zero. However, this cannot be applied universally because, as Whittaker (2010b) points out, a negative relationship across an entire range of productivities for a particular habitat type cannot be represented as unimodal. U-shaped relationships were classified as non-significant because u-shaped relationships have no theoretical explanation (Pärtel et al., 2007). This is not consistent with the classification of negative relationships as unimodal. Following their reasoning for classifying negative relationships, u-shaped relationships should have been classified as positive, or bimodal. Moreover, despite their assertion that there are no explanations for u-shaped relationships, there are reasons to expect u-shaped PSRRs in some cases. Scheiner and Jones (2002) reported a u-shaped plant–PSRR suggesting it may be due to the transitional nature of the habitats of the high and low productivity sites in their study. At ecotones species richness is predicted to be high because of a mixing of species from more than one species pool (Chiba, 2007). Thus if low productivity sites coincide with an ecotone, species richness

might be uncharacteristically high. Gillman and Wright (2006) retained this study and the classification made by Scheiner and Jones (2002), but Pärtel et al. (2007) reclassified it as non-significant despite the possible explanation provided by the primary authors for the u-shape.

Whittaker and Heegaard (2003) took a sample of eight terrestrial tree studies measured at the continental-to-global (i.e. > 4,000km) or regional (i.e. 200–4,000km) scale classified as hump-, u-shaped or negative (from a dataset of 62 studies) by Mittelbach et al. (2001). Of these eight studies, seven were classified by Mittelbach et al. (2001) as unimodal, one as u-shaped and none as negative. After a critical analysis of these studies, Whittaker and Heegaard (2003) found the forms of these relationships were incorrectly classified in all cases. Furthermore, five of the studies were inadmissible as robust tests of the plant–PSRR because Mittelbach et al. (2001) considered annual rainfall as a surrogate for productivity in environments where this was inappropriate. Finally, all three studies that were accepted as robust tests of the plant–PSRR were reclassified by Whittaker and Heegaard (2003) as positive monotonic relationships. Whittaker and Heegaard (2003) concluded with a "call for caution in citing [Mittelbach et al. (2001)'s] findings and for a re-examination of other sections of the meta-analysis."

1.5 Re-analysis of the plant–PSRR (Gillman & Wright 2006)

To date, only the second of the two 'calls' made by Whittaker and Heegaard (2003) has been partially answered. Gillman and Wright (2006) undertook a complete review of the plant–PSRRs presented by Mittelbach et al. (2001) as well as additional studies either missed by Mittelbach et al. (2001) or published after 2000. Following the criticisms made by Whittaker and Heegaard (2003) strict criteria were used for including only

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studies that were robust tests of the plant–PSRR. From the 131 potential member studies, Gillman and Wright (2006) accepted 60 cases as appropriate tests of the plant–PSRR and 18 as tests of a biomass–plant species richness relationship. Accepting less than half the original potential plant–PSRRs highlights the importance of selection criteria for meta-analyses, given that Gillman and Wright (2006) reported that positive relationships were more common than other forms of the plant–PSRR across the whole dataset. Furthermore, positive relationships predominated at continental-to-global and regional extents and at both coarse and fine grains. At the local-to-landscape scale however, the relationships were more variable with positive and unimodal both being relatively common. Similar results were found for biomass–species richness relationships at regional and local-to-landscape extents; there were no continental-to-global biomass–species richness studies. However, Gillman and Wright (2006) reported that biomass explained less variability in species richness than other surrogates (20.8 and 52.6% respectively) indicating that biomass is not a good predictor of species richness. These results contrast with the work presented by Mittelbach et al. (2001) who found that hump-shaped relationships occurred most frequently across the whole dataset, and at all but the broadest extent—positive and hump-shapes co-dominated at continental-to-global extents. Given the criticism by Whittaker and Heegaard (2003), and the subsequent re-analysis by Gillman and Wright (2006) using strict study selection criteria, the results presented by Mittelbach et al. (2001) are unreliable. Therefore, given that Gillman and Wright (2006) considered only terrestrial plant–PSRRs, there is a need for a reassessment of the animal–PSRR.

1.6 Theoretical explanations for the observed patterns of species richness

Theories to explain spatial patterns of species richness can be classified by the mechanisms proposed to generate them. These are ecological, evolutionary, and historical. The following discusses some prominent theories, their predictions and support that they have received. The theories discussed are not an exhaustive list and are restricted to those that invoke energy. The first two theories are ecological in their mechanisms and the third is evolutionary in its mechanism. A fourth theory is presented that operates somewhat independently of energy, is historical in nature and is presented due the recent attention it has received in the literature.

1.6.1 Species–energy theory

The above discussion about productivity and species richness highlights the interest that available energy has received as a potential driver of species richness. This interest began with Hutchinson (1959) when he proposed that places of higher productivity can support more species by supporting longer food chains. Wright (1983) later formalised this idea into species–energy theory. Species–energy theory as proposed by Wright (1983) sought to extend species–area theory (i.e. more area equals more species) by suggesting that larger areas contain more species because they contain more energy. However, species richness increases at a faster rate with energy than with area (Hurlbert & Jetz, 2010; Wylie & Currie, 1993). Nonetheless, the fundamental property of the theory remains the same: more energy can support a greater number of individuals (more individuals hypothesis, Srivastava & Lawton, 1998), allowing for more viable populations, reducing the probability of stochastic extinction. The species–energy hypothesis therefore assumes that productive, species rich places are inhabited by more individuals.

Empirical support for the 'more individuals hypothesis' (MIH) is equivocal. Kaspari et al. (2000) found support for the MIH in ants where both species richness and abundance increased along a gradient of increasing energy. On the other hand, Terborgh et al. (1990) found that the numbers of individuals in bird communities were similar in tropical and temperate regions, but species richness was four to five times higher in the tropics. Interestingly, Mönkkönen, Forsman, & Bokma (2006) found resident bird species increased in abundance and richness with energy whereas migrant birds did not. However, for a hypothesis to be applied to a general pattern, it must be observed generally. Currie et al. (2004) found little support for the MIH as a general explanation for diversity patterns across broad scales. Using tree and breeding bird data, Currie et al. (2004) demonstrated that species richness showed a stronger relationship with AET than total density. Therefore, the MIH cannot be used as a general explanation for the broad scale patterns of species richness.

1.6.2 Physiological tolerance hypothesis

The 'physiological tolerance hypothesis' first proposed by von Humboldt (1808; cited in Hawkins, 2001), states that cold and/or dry places contain fewer species than warm, wet places because only a few species can physiologically tolerate, or survive the 'harsh' conditions. Some argue that the physiological tolerance hypothesis is circular reasoning: high latitudes and hot, dry places are only considered as harsh because of the low diversity and abundance of life in these regions relative to the tropics (Rohde, 1992). However, this is not entirely substantiated. Life is dependent on water, indicating that hot dry places are indeed harsh as are cold places where water can be frozen for extended periods. Biochemical reactions are dependent on liquid water and kinetic energy thus constraining life (particularly poikilotherms) in cold places. Moreover, it

could be argued that there are fewer successful forms found in harsh climates and that specific adaptations are required to tolerate the conditions in them. Schemske (2002) suggests that temperate species have an "optimum phenotype....best characterised as a fixed target" (p. 170) and that even isolated populations would "evolve similar adaptations to cope with the climatic stress" (p. 170). A prediction under the 'physiological tolerance hypothesis' might be that climatic selection pressures are higher in temperate zones resulting in purifying selection purging a greater proportion of mutations in temperate populations than in tropical species. Therefore, species might retain greater genetic diversity in the tropics and this genetic diversity might provide the raw material for greater speciation. Indeed, Chek, Austin and Lougheed (2003) provide some support for this idea with a finding that tropical birds have higher genetic diversity than temperate birds. Furthermore, tropical birds have higher subspecific diversity than temperate bird species (Martin & Tewksbury, 2008). Within species, genetic divergence appears to be greater in lower latitude populations among 60 vertebrate species (Martin & McKay, 2004), within plants (Eo, Wares, & Carroll, 2008), within a fly species in an Australian tropical rainforest (Schiffer, Kennington, Hoffmann, & Blacket, 2007) and at lower elevations in a species of shrew (Ehinger, Fontanillas, Petit, & Perrin, 2002). Nonetheless, in a review of climate-based theories to explain the LDG, Currie et al. (2004) found that the 'physiological tolerance hypothesis' cannot be applied as a universal explanation for spatial patterns of species richness. They demonstrated that despite the absence of obvious dispersal barriers species were absent from regions with suitable climatic conditions (Currie et al., 2004). However, Currie et al. (2004) conclude that direct tests of the 'climate tolerance hypothesis' are few and that further direct tests are necessary to be conclusive.

1.6.3 Evolutionary speed hypothesis

Across broad scales, invoking evolutionary explanations are appropriate, given that total diversity is the consequence of a balance between speciation and extinction (i.e. diversification rate) (Mittelbach et al., 2007). Rensch (1959) proposed that the solar radiation is more intense in the tropics resulting in more mutations and thus more raw material on which selection can act resulting in more adaptive radiations. Therefore, more species accumulate in the tropics because they evolve faster. Rohde (1978, 1992) suggests that evolutionary 'speed' is faster in the tropics because tropical species have greater effective evolutionary time. Rohde's (1978, 1992) greater effective evolutionary time hypothesis of elevated evolutionary rates in warm environments is predicated on three factors: (1) higher temperatures might cause higher rates of mutagenesis; (2) generation time are shorter in tropical regions; and (3) rate of selection will be higher based on the two previous factors. This theory is consistent with observed positive species–energy relationships over broad scales. Warmer temperatures contribute to higher metabolic rates (Gillooly, Brown, West, Savage, & Charnov, 2001), which in turn may cause elevated mutagenesis through production of reactive oxygen species that damage mitochondrial DNA and/or faster cell division increasing the chance of replication error in germ cells (Martin & Palumbi, 1993). However, Lanfear et al. (2007) demonstrated, for 12 different genes and over 300 metazoan species, that after controlling for body size, DNA substitution rate is not influenced by resting metabolic rate. Therefore, the modifying mechanism of temperature on micro-evolution does not appear to be driven by resting metabolic rates. DNA-substitution could however be influenced by annual metabolic rates (Gillman, Keeling, Ross, & Wright, 2009; Gillman & Wright, 2007). Species in temperate and cooler regions often undergo periods of torpor and/or hibernation which slows annual metabolic rates (Song, Körtner, & Geiser, 1995) although this proposition remains to be tested. Nonetheless, shorter generation

times and higher mutation rates might increase the rate of selection thus increasing the rate of microevolution (Rohde, 1992). Importantly however, the link between temperature and DNA substitution requires an explanation.

The evolutionary speed hypothesis (ESH) has received empirical support in both endo- and ectotherms with studies finding elevated rates of microevolution in taxa occupying warmer thermal regimes including: marine Foramifera (Allen, Gillooly, Savage, & Brown, 2006); terrestrial plants (Gillman, Keeling, Gardner, & Wright, 2010; Wright, Keeling, & Gillman, 2006); amphibians (Wright, Gillman, Ross, & Keeling, 2010); hummingbirds (Bleiweiss, 1998); mammals (Gillman et al., 2009) and fish (Wright, Ross, Keeling, McBride, & Gillman, 2011). Gillman and Wright (2006; 2007) proposed that the ESH might potentially explain positive relationships between species richness and productivity if the theory is modified such that evolutionary speed is mediated by both energy and water availability; these being the key factors determining productivity on land. This prediction is consistent with the results presented by Wright et al. (2006) who found higher rates of micro-evolution in plants living at lower latitudes. Furthermore, Goldie, Gillman, Crisp and Wright (2010) recently demonstrated that the tempo of micro-evolution in woody plants in Australia is mediated by water availability. Plants in the dry central regions were found to evolve more slowly than sister species in warm, wet, more productive regions. This further supports the idea that high productivity and not temperature alone is the driver of elevated rates of micro-evolution.

1.6.4 Niche conservatism

Modern techniques in phylogenetics, molecular biology and, the availability of paleontological and biogeographical data means that researchers have become

increasingly interested in exploring evolutionary and historical explanations for diversity patterns (Mittelbach et al., 2007). Historical and evolutionary explanations for broad scale diversity patterns are not new (e.g. Dobzhansky, 1950) and recent work has generated some promising results. From a historical, biogeographical point of view, Latham and Ricklefs (1993) concluded that angiosperm diversity is greater in the tropics since most angiosperm families originated in the late Cretaceous, a time when global climates were predominantly tropical. Therefore, clades that originated in tropical climates have had longer 'effective' time to diversify in a historically larger geographic area resulting in higher diversity in the tropics. This concept has become known as the 'tropical niche conservatism hypothesis' (Wiens & Donoghue, 2004) and is dependent on the assumption that closely related species have more similar niche requirements than distantly related species. In particular, it is posited that clades that originate in the tropics or warm places do not easily evolve the ability to tolerate freezing temperatures and frost (Ricklefs & Schluter, 1993).

Niche conservatism has been tested for a number of taxa including: mammals (Buckley et al., 2010); butterflies (Hawkins, 2010; Hawkins & DeVries, 2009); birds (Hawkins, Diniz-Filho, Jaramillo, & Soeller, 2006); frogs (Wiens, Graham, Moen, Smith, & Reeder, 2006; Wiens, Sukumaran, Pyron, & Brown, 2009); reptiles (Morales-Castilla et al., in press); and angiosperms (Hawkins, Rodríguez, & Weller, in press). Wiens et al. (2006, 2009) tested the tropical niche conservatism hypothesis in two frog families (New World Hylidae and Old World Ranidae). They demonstrated that both of the families originated in tropical regions and subsequently some clades within the families have invaded higher latitudes. Furthermore, the older tropical clades were more diverse than the younger temperate clades. They hypothesise that the historically greater area of the tropics explains why the clades originated there, and that it is difficult for species to evolve cold tolerances which prevents them from frequently invading colder

regions. Therefore, clades in the tropics are more diverse because they have had a longer time to diversify in their ancestral niche compared to clades that have recently moved into temperate zones. Hawkins and DeVries (2009) and Hawkins et al. (in press) have demonstrated similar patterns in North American butterflies and angiosperms respectively. Niche conservatism has also been shown to explain other patterns of diversity across different gradients. Morales-Castilla et al. (in press) found that reptile groups in eastern and southern Africa were more diverse in the climatic habitats that most resemble the conditions in which they originated. Therefore, niche conservatism has the potential to explain gradients in contemporary species richness. Importantly, however, niche conservatism does not need to be considered as mutually exclusive of other mechanisms that might control diversity. The LDG has been shown to have existed for at least 260 Myrs (Crame, 2001) and until relatively recently (~30–40 Myrs ago) the tropics covered the largest geographical extent on Earth. However, even after the expansion of the temperate zone, origination rates have remained higher in tropical regions than temperate regions (Jablonski, Roy, & Valentine, 2006). Therefore, the LDG appears to have, at least in part, arisen independent of tropical niche conservatism and some other mechanism might explain its origination such as faster evolutionary speed and higher diversification rates. Nonetheless, niche conservatism maintains and strengthens the LDG.

1.7 The animal–productivity species richness relationship

Understanding the relationship between productivity and species richness is a key factor in determining why some places have more species than others. Yet, despite the attention that PSRRs have received, there is still disagreement in the literature regarding the influence of scale and the form of the PSRR (Gillman & Wright, 2006; Mittelbach et

al., 2001; Waide et al., 1999; Whittaker & Heegaard, 2003). Much of the disagreement has come from inconsistent methods for evaluating the relationship, but also the way in which scale has been treated (Gillman & Wright, 2006; Whittaker, 2010b; Whittaker & Heegaard, 2003). Among the reviews of the PSRR there is again controversy. The analysis by Gillman and Wright (2006) is the most systematic and critical, suggesting that the results presented by them are robust. However, despite the criticisms and re-analysis, Mittelbach et al. (2001) remains preferentially cited (45.8 citations/yr) in contrast to Whitaker and Heegaard (2003) and Gillman and Wright (2006) (8.3 and 11 citations/yr respectively) (Table 2). While citation frequency for Gillman and Wright (2006) is increasing, the same can be observed of Pärtel et al. (2007). The increasing citation frequency of Pärtel et al. (2007) is somewhat troubling given the short comings of the study discussed above (see *1.4. Critical analysis of PSRR reviews*). The robust nature of the analysis by Gillman and Wright (2006) is a sentiment generally endorsed by Whittaker (2010b) " [Gillman and Wright (2006)] is in substance a worthy and critical reanalysis" (p. 2523). However, there were small inconsistencies in the outcome between a sample of studies (n = 68) analysed by Whittaker (2010b) and the results of Gillman and Wright (2006). Nonetheless, the overall pattern remains unchanged if these inconsistencies are reconciled (i.e. positive relationships predominante) (Gillman & Wright, 2010). The issue raised regarding meta-analyses and the plant–PSRR is therefore somewhat resolved, but the relationship between animal species richness and productivity remains unclear.

Table 2. The number of citations per year (in *ISI Web of Science*) of the three PSRR reviews, including the critical analysis by Whittaker and Heegaard (2003).

	Paper			
Year	M2001[†]	WH2003[§]	GW2006[‡]	P2007[*]
2001	0	na	na	na
2002	16	na	na	na
2003	51	1	na	na
2004	45	3	na	na
2005	54	15	na	na
2006	61	10	1	na
2007	60	9	9	0
2008	50	8	12	9
2009	68	7	11	6
2010	63	13	22	13
Total citations	468	66	55	28
Citations per year	46.8	8.25	11	7

[†]Mittelbach et al. (2001); [§]Whittaker and Heegaard (2003); [‡]Gillman and Wright (2006); [*]Pärtel et al. (2007)

Here a meta-analysis of all animal–productivity species richness relationships (A–PSRR) published up to 2010 is presented. This includes a re-analysis of the animal dataset used by Mittelbach et al. (2001) (88 independent cases of the A–PSRR from 58 studies), as well as additional studies published after September 1999 (298 independent cases of the A–PSRR from 233 studies), and studies missed by Mittelbach et al. (2001) (19 independent cases of the A–PSRR from 12 studies). This re-analysis builds on the work of Whittaker and Heegaard (2003) and Gillman and Wright (2006) in an attempt to critically asses the A–PSRR. The issues of scale dependency, productivity surrogates and statistical methods discussed above are addressed. Additionally, strict criteria are used for selecting studies that are robust tests of the A–PSRR. Of the previous reviews, only Mittelbach et al. (2001) used formal meta-analytical techniques, albeit in a limted way. Therefore, in this study, additional meta-analytical methods are employed to test the comparative strengths of different relationships across the whole dataset, different scales (grain and extent), different ecosystems (terrestrial, freshwater and marine), and homeo- and poikilotherms. The results of these analyses are then compared to the

results presented by Mittelbach et al. (2001) and, any inconsistencies or similarities are explained in terms of the difference in size and composition of the datasets, selection criteria, and the methods for classifying relationships. Finally, potential explanations are discussed that might account for the observed patterns in the A–PSRRs.

2. INTRODUCTION TO META-ANALYSIS

The scientific literature is filled with studies asking the same or similar questions and often the conclusions from these studies will not be in agreement, particularly in highly researched fields that can have hundreds of broadly similar studies. This can lead to uncertainty about the generality of observed phenomena and whether responses change across various conditions. There are numerous reasons why researchers replicate studies and although the key reason is to test the generality of phenomena, other reasons include: an unawareness of similar work, a dissatisfaction with the methods used by others, or an attempt to expand current knowledge in their area of interest (Cooper & Hedges, 2009). Literature reviews are a common way to assess broad questions and while narrative reviews can provide some insight toward generalising answers to these questions, they lack a formal statistical framework to make robust inferences. Meta-analysis, the quantitative summary and analyses of a number of independent studies (Hedges & Olkin, 1985) on the other hand provides the statistical framework to do so. Although meta-analyses have been widely used in some fields of science, particularly medicine and epidemiology, the technique is relatively new to ecological research. Meta-analyses were first used in ecology in the early 1990s (Gurevitch & Hedges, 2001) and have become increasingly common (Hillebrand, 2008). Using "meta-analysis" as a *topic* keyword in *ISI Web of Science*, 626 articles in ecology were identified between 1990 and 2010, with a clear trend of increasing annual frequency (Figure 2). This trend is undoubtedly mirrored by the number of individual studies in ecology, particularly those addressing controversial topics such as the drivers of species diversity patterns. It is therefore ever more important to attempt to synthesise results to investigate whether or not general patterns can be derived from these individual studies.
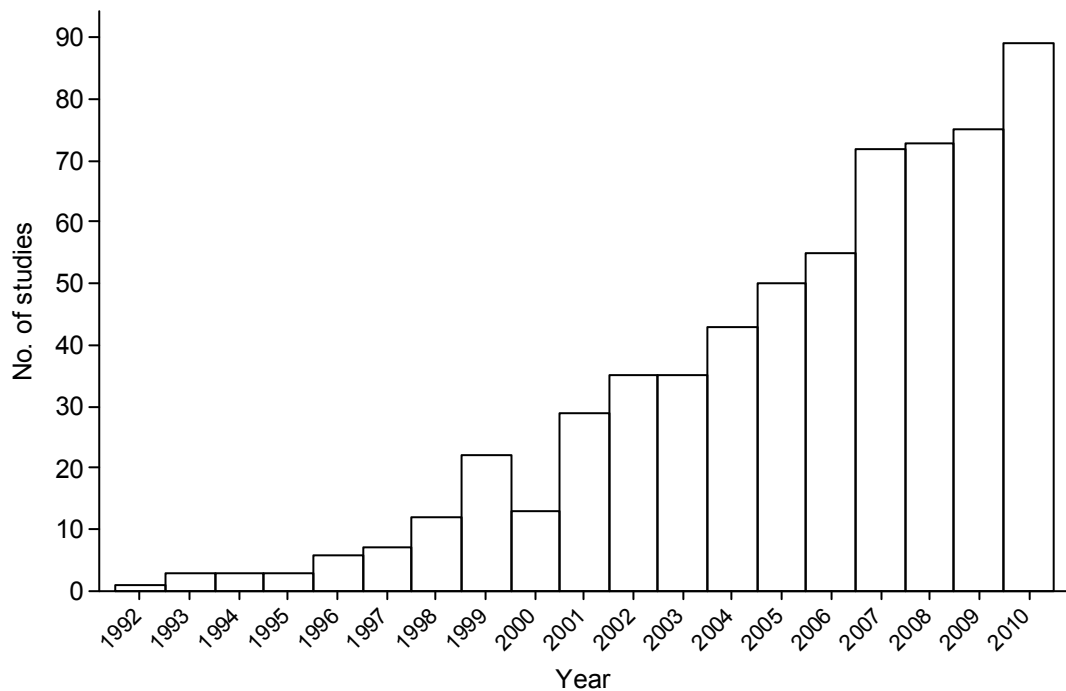
Figure 2. The number of studies with "meta-analysis" as a topic per year between 1991 and 2010 in ecological research in *ISI Web of Science.*

2.1 Vote-counting

Vote-counting was initially the most commonly used method for ecological research synthesis (Gurevitch & Hedges, 1999) whereby individual studies are tallied with equal strength according to their response to a particular "treatment". For example, a meta-analyst has a group of 20 studies that studied the response of organism A to factor B. In 11 of the studies organism *A* displayed an increased growth rate, in seven of the studies organism *A* displayed a decreased growth rate and, in two of the studies there was no difference between the growth rates of the treatment and control groups. Given these results, a vote-count would conclude that in general, organism *A* has a faster growth rate when exposed to factor B. In reality the difference between positive and negative responses is small and no account is taken of the strength of the effect. Large studies tend to have significant results, a result of sample size regardless of the size of the

effect. Small studies on the other hand are more likely to be non-significant, again an artefact of sample size. This can lead to an inflation of type II errors (i.e. failing to reject a null-hypothesis when it is false), one of the main criticisms aimed at vote-counting (e.g. Friedman, 2001; Gurevitch & Hedges, 1999). It therefore makes sense to use other methods that account for strength and sample sizes of member studies. However, there are two important considerations to make. Firstly, as Bushman and Wang (2009) point out, "not all vote-counts are created equal", and using vote-counts in conjunction with effect sizes (see *2.2 Meta-analysis* for description of effect size) can add robustness to an analysis, particularly where effect sizes cannot be calculated for all member studies. Secondly, vote-counting can be informative if a consistent response is reported across a range of different conditions (e.g. scales) or as an exploration of the overall patterns in the dataset (Gurevitch & Mengersen, 2010).

2.2 Meta-analysis

The alternative to vote-counting is a formal meta-analysis in which studies are weighted by their effect size. An effect size is a statistical measure of the response that the dependent variable has in relation to change in the independent variable (Cooper et al., 2009), which can be standardised or weighted by sample size for meta-analyses. Effect sizes can be calculated from traditional statistical results (e.g. correlations). Harrison (2011) elegantly refers to effect sizes as the *P*-values and the cornerstone of meta-analysis and while it is indeed true that a weighted meta-analysis is the gold standard to which literature syntheses should be held, it is not without its difficulties. One of the main difficulties to overcome relates to data availability. The optimum approach would be re-analysing raw data from each study in a standardised way that addresses the question being asked, allowing direct comparisons between studies. Generally however,

journals have limits on article length, making it impossible to publish raw data tables.

Therefore, it is only practical to publish small datasets in the body of an article.

Fortunately, publishing raw data has become more common in ecological research with

the use of online data supplements, but whole datasets are rare and it is a nontrivial and

time-consuming endeavour to re-analyse the data from all member studies. Data for re-

analysis can also be obtained by digitising published figures using software such as

DataThief (Tummers, 2006) although some errors can occur due to over-plotted data

(Whittaker & Heegaard, 2003). Finally, if data cannot be re-analysed, coefficients can

be extracted from the results published in the paper. The drawback of this approach is

that authors are not always explicit about the methods used for analyses or, important

statistics from which appropriate effect sizes can be calculated (e.g. sample sizes,

correlations etc.) are not reported. Therefore, studies from which effect sizes cannot be

calculated, or no meaningful response can be determined, must be excluded from the

final meta-analysis. This can unfortunately reduce the eventual number of studies in the

dataset, potentially influencing the final outcome. In extreme cases, the general nature

of the conclusions can be brought into question as a result of the high number of studies

that are rejected due to unavailable data.

2.3 Study selection

While study syntheses are greatly strengthened by sound meta-analytical methods, if the

data is substandard the final outcome may be misleading. Therefore, judging the quality

and appropriateness of potential member studies is an important part of the systematic

review process. Including studies that are inappropriate to the question being asked is

likely to introduce error and lead to erroneous conclusions (Harrison, 2011). However,

how does one assess the appropriateness of a study? The key element of member studies

is whether they suitably address the underlying question the meta-analyst is asking. Studies are rarely exactly the same in aim and methodology; making it important to carefully read each member study to identify any difference, and to determine if the studies are indeed comparable. Moreover, there may be confounding variables that have a strong influence on the dependent variable, down-playing or distorting the importance of the variable the meta-analyst is interested in. Therefore, after identifying potential member studies, each study needs to be critically assessed for inclusion using a set of predetermined, scientifically defensible criteria (Englund, Sarnelle, & Cooper, 1999; Gurevitch & Hedges, 2001). In the ecology discipline, this point has been highlighted by a forum in *Ecology* regarding meta-analysis of the relationship between productivity and species richness (e.g. Gillman & Wright, 2010; Hillebrand & Cardinale, 2010; Whittaker, 2010b). In the case of the PSRR, two meta-analyses (Gillman & Wright, 2006; Mittelbach et al., 2001) had contrasting results, in part due to inappropriate or more lax study selection criteria, on the part of Mittelbach et al (2001) (Gillman & Wright, 2006; Whittaker, 2010b; Whittaker & Heegaard, 2003). An interesting study (Werenkraut & Ruggiero, 2011) addressed the issues of selection criteria application in species richness gradients; a meta-analysis of the species richness–altitude relationship using stringent, intermediate and lax selection criteria to compare how selection criteria influence the final outcome. The results from the varying degrees of relaxation in selection criteria were in contrast to each other, further cementing the assertion in using appropriate selection criteria.

2.4 Publication bias

Publication bias is the selective publication of studies with certain results (Begg, 1994) and is of concern for meta-analysts (Hillebrand, 2008). As mentioned with regard to vote counting, studies with non-significant responses are rarely published which can introduce publication bias (Greenhouse & Iyengar, 2009). Rosenthal (1969) referred to this as the 'file drawer' problem**,** imagining that authors filed these non-significant studies away rather than publishing them. In addition to filing these studies away, many studies may test the influence of a number of variables but only report the results of the significant or "best" (i.e. strongest influence) variables. For example, Hawkins et al (2003) tested the influence of a number of climatic variables on bird species richness but only reported either the results of the best multiple variable regression models or, the results of the best single variable regression. Publication bias to some degree is generally unavoidable. Therefore, the meta-analyst needs tools to assess the presence of publication bias. There are two suggested methods to assess the presence of publication bias, (1) a graphical representation of the data called a funnel plot and, (2) a statistical analysis called the fail-safe measure. A funnel plot is a scatterplot of sample size verses effect size, named after the symmetrical funnel form an unbiased meta-analysis should show (Sutton, 2009). The funnel form is an artefact of studies with large sample sizes typically being less numerous and having less variable effect sizes compared to studies with small sample sizes (Figure 3). Non-significant studies typically have small effect sizes, thus a meta-analysis with publication bias against small effect size will have missing data at the lower end of the effect size (Figure 4) (Greenhouse & Iyengar, 2009).
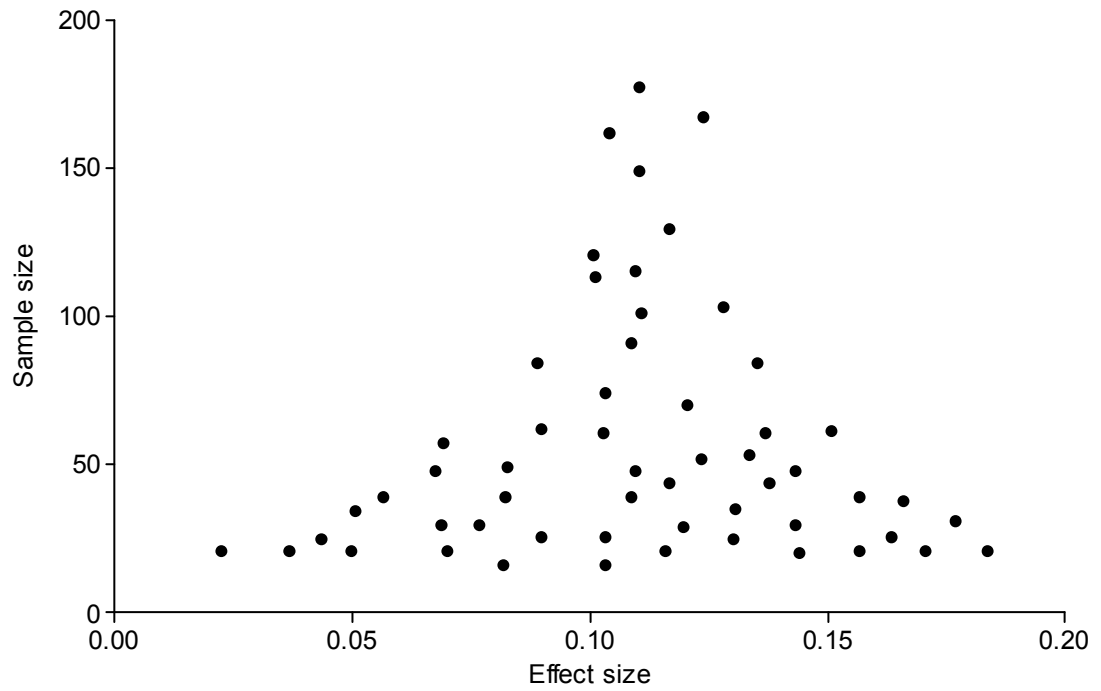
Figure 3. An example of a simulated funnel plot of an unbiased meta-analysis with a symmetrical funnel form.
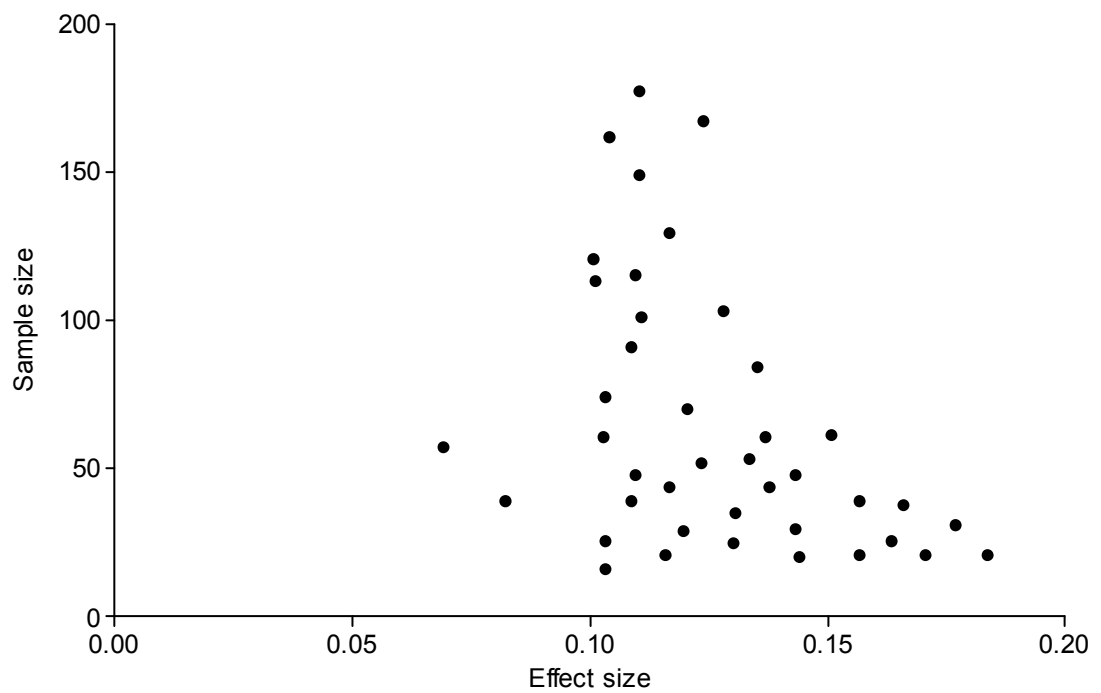
Figure 4. An example of a simulated funnel plot of a meta-analysis with bias against studies with small effect sizes, indicated by the skewed, non-symmetrical form.

The most commonly used method for determining the presence of publication bias in the form of the file drawer problem is by calculating a fail-safe number (Rosenberg, Adams, & Gurevitch, 2000). Fail-safe numbers reflect the potential number of unpublished or non-significant studies that would be required to change the results of the meta-analysis (Greenhouse & Iyengar, 2009). A large fail-safe number, relative to the number of member studies, would therefore mean that the meta-analyst can be confident that the obtained results are representative of the true population effect size.

2.5 Conclusion and summary

Research synthesis using systematic review techniques can be regarded as an independent scientific discipline since it follows the general scientific method (Cooper et al., 2009). A question or hypothesis is defined, data is collected (member studies), the data is analysed in an accepted manner and the results are interpreted and framed in reference to the tested hypothesis. Importantly, as with other research projects, studies need to have the added element of being repeatable. Therefore, a sound and explicit protocol for meta-analysis should be followed. The following are general steps that should be followed when undertaking a systematic review and meta-analysis to meet the criteria of a robust and repeatable scientific study (modified from Harrison, 2011):

1. Execute an extensive literature search for potential member studies using appropriate keywords. Where possible, to avoid the file drawer problem, it is advisable to attempt to obtain unpublished non-significant results because of the tendency of authors to not submit, or for journals to reject non-significant results (Csada, James, & Espie, 1996; Rosenthal, 1969).

2. Enter the studies into a master database, recording important information (e.g. taxa or habitat type). Critically scrutinise each member study for

appropriateness in answering the initial research question using *a priori* criteria. Reject those that fail to meet the criteria noting the reasons for non-inclusion. Note any interesting features of accepted studies.

3. Determine the appropriate effect size statistic and calculate it where possible.

4. Perform meta-analytical techniques on the calculated effect sizes to determine if the hypothesis is supported or not. Identify any interesting anomalies or similarities across the dataset and attempt to explain them.

5. Assess the robustness of the analysis checking for publication bias, something which can arise from the aforementioned 'file drawer' problem. Techniques such as funnel plots and fail-safe sample sizes can be used.

In order to move forward in any scientific discipline researchers need to build on the work of the past and while undertaking the same or similar studies over and over may be somewhat informative, there comes a time where conducting more research around a particular question adds little to the over-all understanding. The exciting part however, is that each of those studies provides raw data that can be synthesised into a general picture. The strength of a well-framed and executed literature synthesis and meta-analysis is undoubtedly a promising option for moving forward and can be highly informative within the field of interest. This sentiment is echoed by Hillebrand and Cardinale (2010, p. 2546) in their statement about the state of research synthesis in ecology, that they " are generally enthusiastic that ecology as a discipline has moved beyond the case studies and contingencies of individual systems to seek generality."

3. METHODS

Two methods were used to assess what the most common and strongest form of the A–PSRR is. The first methods involved a vote-count (see *2.1 Vote-counting*) to determine which form of the A–PSRR is most common among different geographic extents, sampling grains, ecosystem types and homeo- and poikilotherms. Then, within the same categories as the vote count, the strength (effect size) of the different forms of the A–PSRR were assessed using meta-analytical techniques (see *2.2 Meta-analysis*).

3.1 Collecting the member studies

3.1.1 Keyword search

The studies for inclusion in the meta-analysis were collected from two sources. First, all the animal–productivity species richness (A–PSR) studies reported in Mittelbach et al. (2001) were obtained. Secondly, published A–PSR studies were assembled from the literature using an electronic keyword search in *ISI Web of Science*: "species richness" OR "species diversity" AND each of the following, productivity, energy, "actual evapotranspiration", rainfall, precipitation, biomass and elevation. Additional studies were also identified from citations in published studies. Studies where productivity was artificially manipulated were not included in the dataset. The keywords used were also likely to find papers that did not specifically test the A–PSRR, or tested a range of other variables (e.g. rainfall–species richness) but, where data were available; these studies were preliminarily accepted.

3.1.2 Study grouping and selection criteria

Studies were classified into broad categories relating to scale, taxon and area of study. Scale was defined in two ways: (1) extent as local-to-landscape (0–200km), regional (200–4000km) or continental-to-global (>4000km) and, (2) sampling grain as either fine (alpha or point diversity) or coarse (beta diversity or whole communities). Animals were first placed in broad taxonomic groups (e.g. birds or mammals etc.), and then classified according to thermal physiology (homeo- or poikilothermic) and skeletal structure (invert- or vertebrate). Each study was critically assessed for inclusion in the final analyses using the following selection criteria: (1) a constant sampling regime was maintained across the study; (2) study sites were not substantially influenced by anthropogenic disturbance; (3) study sites were not substantially altered by introduced species; (4) the surrogate for productivity is appropriate for the system being studied, and not liable to distortion from other factors; (5) the study design was not likely to influence the perceived A–PSRR; (6) the entire dataset, or part thereof, was not included more than once; (7) no other study assessing the A–PSRR has been included that covers the same taxon across the same spatial area; (8) the target taxa were not phylogenetically restricted; and; (9) the sample size of the study was greater than 10; Additionally, studies could not be included in the final meta-analysis where data were not available. The justification for the choice of selection criteria is discussed below including examples where available. A full discussion of all studies that were rejected is included in *Appendix 1*. It should be noted, however, that rejection of a study for this meta-analysis does not infer that the study in question was faulty; only that it was not suitable for the questions being addressed here. Criterion five, relating to study design is not discussed because it is a general criterion that is embedded within many of the other criteria. For example, unequal sampling effort or variable area is a component of study design that can influence the form of the observed relationship.

3.2 Justification of selection criteria

3.2.1 Unequal sampling or variable area

An increase in species richness with an increase in area, called the species–area curve, is a well-documented phenomenon in ecology (Lomolino, Riddle, & Brown, 2005; Rosenzweig, 1995), so much so that it has been described as "one of community ecology's few laws" (Schoener, 1976). Indeed the increase in diversity with area is a foundation principle of one of the first unifying theories is ecology; the theory of island biogeography (MacArthur & Wilson, 1967). There are two reasons for the increase of species richness with area: (1) as more area is sampled, more individuals are sampled, increasing the chance of encountering 'new' species and, (2) larger areas are likely to be more environmentally heterogeneous, thus supporting more species that differ in their niche requirements (Hill, Curran, & Foody, 1994; Scheiner, 2003). Generally the form of the species–area curve is assumed to be an increasing power function but this is not always true (Scheiner et al., 2011), and there are ~20 different proposed models to describe the species–area curve including asymptotic and non-asymptotic curves (Tjørve, 2009). Nonetheless, it is clear that area influences species richness positively, and when attempting to identify ecological reasons for differences in species richness, both sampling effort and area of sampling sites needs to be held constant to avoid the confounding effect of area. A number of studies were excluded from the dataset due to unequal sampling effort and variation in the area of sampling sites. For example, Bachelet et al. (1996) sampled marine sediments across different depths using three coring devices that differed in size. The smallest device ($0.0216m^2$) was used in the shallower waters (2-7m) with fine grain sized sediments, the intermediately sized device ($0.04m^2$) in shallow water with coarse sediments and the largest device ($0.1m^2$) in deeper water ($\geq$ 10m). Given that an equal number of replicates were taken with each

device at the different depth and sediments, the sample area at deeper sites was over four and a half times greater than shallow, fine sediment sites. Therefore, there is the potential for inflated species richness at the deeper sites due to the level of sampling effort. Indeed there was an increase in diversity with depth suggesting that sampling effort may have influenced the result.

3.2.2 Anthropogenic influence

Patterns of biodiversity have until modern times been shaped by natural processes including speciation, extinction, dispersal and species interactions. However, as the human population grows, anthropogenic activities are having increasing effects on natural systems and processes (Vitousek, Mooney, Lubchenco, & Melillo, 1997). The types of activities can be conspicuous and dramatic, such as the clearing of a forest, or they can be more subtle and seemingly benign, such as agricultural runoff entering a lake via a large catchment. The aim of this work was to classify the form of the A–PSRR under conditions relatively free from anthropogenic influence. Thus, species richness data influenced by anthropogenic activity needed to be excluded or at least minimised. Fifty-six studies were excluded from the dataset due to anthropogenic activity. In particular, studies of the A–PSRR in freshwater systems were excluded due either to pollutants that were discharged directly into the waterway (e.g. Rebelo, 1992) or, waterways that had nutrient enrichment from development (Dodson, Arnott, & Cottingham, 2000) or agriculture (Leibold, 1999). It is surprising that despite having the criterion of excluding studies that were subject to severe anthropogenic disturbance, Mittelbach et al. (2001) chose to not exclude Rebelo (1992) given the explicit assertion that "[t]he substantial development of industries and population in the watershed, with only minor effluent treatment, coupled with intense activities of the industrial and

fishing port, are the principle sources of pollution to the lagoon" (Rebelo, 1992, p. 404). Furthermore, the pollutants discharged undoubtedly had an influence on biodiversity and include: organic and chemical pollution from paper-pulp factories, mercury pollution from industrial activities and, human and cattle effluent (Rebelo, 1992). Another study, excluded here but not available to Mittelbach et al. (2001), was Dodson et al. (2000). Dodson et al. (2000) found a unimodal relationship for three aquatic invertebrate groups. However, some of the lakes had watersheds that contained anthropogenic development. Importantly, Hoffman and Dodson (2005) showed that there was a difference in the A–PSRR in zooplankton between pristine lakes and lakes with developed watersheds; pristine lakes had positive relationships, developed lakes had negative relationships, and when the two were combined there was a unimodal relationship. Thus, the appearance of unimodal relationships in Dodson et al. (2000) cannot be interpreted as a natural A–PSRR.

3.2.3 Introduced species influence

Introduced species can influence natural communities, and sometimes the effects can be substantially negative (i.e. reduction in the diversity of native/endemic species). Exotic species influence invaded areas through competition for resources or predation (Shea & Chesson, 2002). The magnitude of influence an invader has on the community is dependent on population growth rate and density, which in turn is regulated by niche opportunity. Niche opportunity is the potential that an area has to support a given invader and is related to resource availability, enemies or competitors and, the physical conditions of the invaded environment (Davis, Grime, & Thompson, 2000; Shea & Chesson, 2002). Thus, when an invader is introduced to an area with sufficiently abundant resources, few enemies or competitors and suitable environmental conditions,

it is likely to be successful and have some influence on the existing natural community. In the dataset, one study that was rejected due to substantial influence from an introduced species—amongst other reasons such as, suburban runoff— was Hobæk et al. (2002). Many of the lakes used in the study contained introduced pike (*Esox lucius*), a voracious predator native to much of Europe; the study was undertaken in Norway. Therefore, given that the environmental conditions were most likely suitable due to being in the pike's potential native range, and the pike's dominance over other predatory fish in the region (e.g. brown trout, *Salmo trutta*), it is unsurprising that populations of native fish were either greatly reduced or locally extinct (Hobæk et al., 2002).

3.2.4 Appropriate use of productivity surrogates

Fundamentally, productivity is the biomass accumulation per unit area per unit time (e.g. $g/m^2/yr$) or the rate at which energy flows through a system (e.g. $kj/m^2/yr$). Practically however, the above measures are difficult to quantify. For example, to measure biomass accumulation requires removal of all the present biomass followed by a measurement of biomass after a given time period. For some taxonomic groups this may be possible such as, annual plants, but even then confounding factors such as browsing/grazing need to be accounted for or controlled. However, the removal of the entire biomass (i.e. reduction in diversity) from an area will invariably affect the potential of that area to produce biomass (Cardinale, Bennett, Nelson, & Gross, 2009). In animals, biomass is commonly measured in dry weight, but this is time consuming, and clearly impractical and excessively destructive for large bodied taxa. Therefore, proxies or surrogates are used to make estimation of productivity more practical for ecological research (Rosenzweig & Abramsky, 1993). In terrestrial ecosystems, actual

evapotranspiration (AET) is commonly used as a surrogate for productivity. AET is a balance between water and energy that is closely related to net primary productivity in a range of climatic regimes (Rosenzweig, 1968). AET is measured as the amount of water transferred to the atmosphere through the process of evaporation and transpiration, thus reflecting the productive activity of plants in the given water and energy regime. Other proxies for productivity used in the literature include, rainfall and potential evapotranspiration (PET), but unlike AET, neither can be applied generally. Rainfall is only appropriate in arid or semi-arid environments where water is the limiting factor for growth (Rosenzweig & Abramsky, 1993), and conversely PET is only appropriate where water is not the limiting factor for growth (Hawkins, Porter et al., 2003).

In aquatic ecosystems, the surrogates are different from those used in terrestrial ecosystems. Surrogates used in freshwater ecosystems differ from those used in marine systems which probably reflect the practicality of measurement due to access and scale. Nutrient content (e.g. nitrogen and phosphorous) and chlorophyll *a* concentration are commonly used surrogates in freshwater systems. Indeed an increase in limiting nutrients such as nitrogen and phosphorous does contribute to productivity in freshwater systems. However, nutrient concentration may not have a linear relationship with productivity; as productivity increases algal and phytoplankton concentrations increase, reducing water transparency. Since productivity relies on light for photosynthesis, decreasing transparency can lead to self-shading resulting in a decelerating curve with productivity levelling-off with increasing nutrient concentrations (Smith, 1979).

Excess nutrients in waterways can cause eutrophication, potentially leading to hypoxia and acidification, which can kill aquatic animals such as fish and zooplankton (Camargo & Alonso, 2006). Although eutrophic and hypereutrophic water bodies theoretically have high algal biomass production, an over-abundance of nutrients can

have adverse effects on biodiversity (Smith, 2003). Additionally, eutrophication can cause the composition of the phytoplankton to shift and can include toxic, bloom-forming cyanobacteria (Smith, 2003). Importantly, the source of excess nutrients in aquatic ecosystems must be considered, due the strong correlation between nitrogen and nitrate export and human population density (*3.2.2 Anthropogenic influence*) (Vitousek, Aber et al., 1997). Therefore, it was important to determine if the source of nutrient enrichment was substantially anthropogenic in studies using nutrients as a surrogate for productivity. Moreover, studies that had waterways with high nutrient concentrations related to eutrophication were excluded to avoid the confounding influence of toxicity.

An example that was excluded here for the aforementioned combination of anthropogenic–nutrient source, but included by Mittelbach et al. (2001) , is Leibold (1999). Leibold (1999) found a unimodal relationship between species richness of zooplankton and phosphorous concentration in a series of ponds. However, four of the ponds were artificial, including eutrophic, disused diary-effluent settlement ponds. Despite the assertion that the artificial ponds had been undisturbed for at least eight years, dairy effluent ponds represent extreme cases of anthropogenic eutrophication that would likely be toxic environments. Therefore, low diversity in the ponds with high phosphorous concentration (i.e. the downward turn of the curve) could reflect two mechanisms other than productivity; (1) high toxicity; (2) eight years is unlikely to be sufficient time for complete re-colonisation.

In marine studies, depth is a commonly used surrogate for productivity; the underlying assumption is that an increase in depth represents a decline in productivity (Rosenzweig & Abramsky, 1993). In general this cline holds true for two linked reasons. Firstly, light penetration decreases with depth, and since light is essential for primary production, deeper water has lower productivity than shallower water.

Secondly, since there is no primary production in the euphotic zone, life is dependent on the export of organic matter from the photic zone for an energy source. Importantly, both biomass and the amount and quality of particulate organic matter that reaches the seafloor decline with depth (Pace, Knauer, Karl, & Martin, 1987; Wei et al., 2010) indicating a gradient in productivity. However, depth cannot be universally applied as a surrogate for productivity. In coastal waters, despite having a potential for higher productivity, shallower water can be highly stressed environments exposed to constant wave action, periodic storms and siltation (Loya, 1972, 1976). Four studies were excluded from the dataset for this reason, all of which compared coral species richness with depth (Huston, 1985; Loya, 1972; Porter, 1972; Sheppard, 1980).

3.2.5 Data duplication

Including the same data or a subset of the same data in a single meta-analysis is intuitively problematic similar to within-study data replication. Nonetheless, it can be a simple mistake to make, particularly when authors have not been clear about data sources. The literature can contain numerous studies that analyse the same taxonomic group across the same spatial scale and can be done for different reasons. For example, modern online databases such as the WildFinder database (WWF, 2006) and the International Union for Conservation of Nature Red List have made collection of species distribution data relatively straight forward. Therefore, researchers might undertake the same or broadly similar studies to those that have been done in the past because of the higher quality, greater coverage and easily accessible modern datasets. Modern spatial analysis techniques allow rapid and thorough analyses to be undertaken. Therefore, different studies might include different variables, but also the same or similar variables (e.g. productivity represented by AET or Normalised Digital

Vegetation Index (NDVI) might be included to test their relative explanatory power or, to build multivariable predictor models. For example, using *a priori* knowledge that species richness is related to AET (Currie et al., 2004; Hawkins, Field et al., 2003), Storch et al. (2006) tested the mid-domain effect (MDE) against productivity (AET) at predicting global bird species richness —AET was first tested against a measure of net primary productivity and NDVI to determine the best 'productivity' predictor. Previously however, Hawkins et al. (2003) had also examined the relationship between AET (and other climate variables) and global bird species richness. Therefore, it was inappropriate to include both studies. Here the most recent study (Storch et al., 2006), assumed to have the most up-to-date dataset, was used preferentially. Furthermore, raw data were available for the chosen study, making re-analysis uncomplicated and reliable without having to digitise the figure from Hawkins et al. (2003), which can introduce error (Whittaker & Heegaard, 2003). A further two studies were excluded that covered the same taxon and geographic scale. In addition, 15 studies were excluded that used either the identical data to answer a slightly different question, or used the same data source for species distributions.

3.2.6 Taxonomic restriction

Species differ in their niche requirements and a component of that niche will certainly include climatic conditions related to productivity. Furthermore, derived species tend to retain characteristics of the fundamental niche of their ancestral species over time (Wiens & Graham, 2005) and be ecologically similar (Burns & Strauss, 2011). That means that over time, as a group radiates, species are more likely to remain in the environment in which the group originated. For example, in eastern and southern Africa, Morales-Castilla et al. (in press) found that the contemporary diversity of

squamate reptile groups is elevated in climatic conditions that are similar to the conditions in which the group/s originated/radiated. In this case older groups originated in predominantly arid climates whereas the younger groups originated in equatorial climates. In the dataset 18 cases were excluded due to taxonomic restriction. Eleven of the cases were from a single study (Terribile et al., 2009) aimed at investigating the influence of history and ecology on diversity patterns of two snake families. Mittelbach et al. (2001) included Davidowitz and Rosenzweig (1998) and, using latitude as a surrogate for productivity, classified the form of the relationship as unimodal. However, the taxon used for the analysis was restricted to three subfamilies of acridid grasshoppers. The importance here lies in the explicit suggestion made by the authors regarding the habitat specificity of acridid grasshoppers and how it related to the observed pattern of species richness. Two of the subfamilies live in prairie habitats and rarely occur in forests. Given that the lower range of latitudes covered in the study were tropical forest, and the mid-latitude ranges were predominantly prairie, a unimodal form is unsurprising and does not reflect the influence of productivity but rather taxonomic habitat preference. This study also suffered from unequal sampling effort.

3.2.7 Sample size ≥ 10

The power to detect a statistically significant pattern is related to the sample size. Therefore, following Mittelbach et al. (2001) and Gillman and Wright (2006) for consistency, a minimum sample size of 10 was employed. Hillebrand and Cardinale (2010) argue that excluding studies with small sample sizes from meta-analyses is unnecessary given that meta-analytical techniques weight effects sizes by sample size. On the other hand, studies with small sample sizes introduce noise to the overall dataset and reduce the power of the meta-analysis (Harrison, 2011). A potential method for

dealing with studies with small sample size might be to conduct the analysis first including all studies, and then excluding the studies with small sample sizes in order to examine the influence of sample size (Harrison, 2011). Using the cut-off of 10 a large number of studies (83) were excluded from the dataset; this constitutes a substantial amount of work that would have been excessively time consuming, and their likely minimal contribution to the final meta-analysis. Furthermore, the process of fitting either a linear or curvilinear line through five or six points is problematic when the form of the relationship is the critical point of interest (Whittaker, 2010a).

3.2 Collecting the data

After determining which studies were robust tests of the A–PSRR, the form of the relationship (i.e. positive, negative, unimodal, u-shaped or non-significant) from each individual member study was determined. Best practice for meta-analysis is to re-analyse primary data from each study to have standardized and comparable results between studies (Gurevitch & Mengersen, 2010). Therefore, studies were first examined for either a data table or an online supplement containing relevant raw data. Where no raw data were published, either within the body of the paper or in an online supplement, an attempt was made to contact corresponding authors to request the data to re-analyse. There were two situations in which data could not be obtained, (1) the studies were relatively old and data were no longer available or, (2) authors could not be contacted or would not share data. In these situations the studies were searched for published figures of the relationship between species richness/diversity and the productivity surrogate. Figures were then carefully digitized using DataThief (Tummers, 2006). If no figure was published, but simple ordinary least squares (OLS) regression results were published (i.e. r-square and significance levels) and authors explicitly stated the form of

the relationship, these results were accepted. Where no simple regression OLS regression results were published (e.g. partial regression coefficients, GLM or spatial regression coefficients) and a relationship was explicitly reported, the final relationship was accepted. However, although these studies could be included in the initial vote count, the results could not be used for final statistical meta-analyses due to a lack of consistency in the methods of analysis.

3.4 Classifying the form of the relationships

After determining which studies were robust tests of the A–PSRR, and data were obtained, the form of the relationship (i.e. positive, negative, unimodal, u-shaped or non-significant) was determined using OLS regression. OLS regression was used in favour of generalised linear models (GLM) used by Mittelbach et al. (2001). GLM assumes Poisson distributions of the data, which is common in ecological data. However, a Poisson distribution also assumes that the variance does not exceed the mean (i.e. overdispersion); an assumption commonly violated in ecological data that can lead to excessively liberal tests (Crawley, 1993). Whittaker and Heegaard (2003) demonstrated that GLM analysis can artificially increase the proportion of studies classified as unimodal.

After testing for a significant quadratic relationship, Mittelbach et al. (2001) applied an additional test of unimodality, commonly called the MOS-test (Mitchell-Olds & Shaw, 1987). The MOS-test tests whether the 95% confidence interval of the peak (or trough) in the data falls within the observed range of values. This however, is 'almost always the case' even when the quadratic term is non-significant (Murtaugh, 2003, p. 613) suggesting that regardless of whether a relationship is truly unimodal, the MOS-test will invariably conclude a hump- or u-shape for curvilinear relationships.

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The above issues relating to the statistical methods used by Mittelbach et al. (2001) suggest that a different approach is required. Firstly, data were visually examined to get a basic form of the relationship prior to performing the regression analyses. Then regression analyses were performed using a fitted line plot, initially using a linear, and then using a quadratic fit. Studies that reported a significant quadratic component ($P < 0.05$) were then checked for a hump- or u-form using locally weighted sums of squares plots (LOWESS) to determine the overall trend in the data. Some studies displayed curvilinear relationships with significant quadratic terms but were neither unimodal nor u-shaped (i.e. decelerating positive, accelerating positive, decelerating negative or accelerating negative). Therefore, to determine the most parsimonious model, corrected Akiake Information Criterion (AICc; Burnham & Anderson, 2002) were calculated for linear and curvilinear models where a lower value corresponds to a better fit. This process was important since the historical assumption of ubiquity with regard to unimodal PSRRs (see *1.2 Energy and species richness*) (e.g. Rosenzweig, 1992; Rosenzweig & Abramsky, 1993) may have led authors to conclude that decelerating positive relationships must be unimodal, and that a wider productivity range would result in a down-turn in diversity at higher productivity levels.

3.5 Vote-count

Once the form of the relationships of each member study had been determined an examination of the data was performed using a vote count. In a meta-analysis of the altitude–species richness relationship, Werenkraut and Ruggiero (2011) showed that the proportions of different relationships varied in relation to the strictness of selection criteria. Therefore, the data was examined before and after applying the selection criteria (discussed above). The proportions of different A–PSRRs (i.e. positive,

negative, unimodal, u-shaped or non-significant) were compared: (1) across the entire

dataset using all the studies for which the form of the relationship could be roughly

determined (i.e. prior to applying the selection criteria discussed above); (2) after

applying the nine selection criteria; and (3) after applying the final criterion of data

availability. Using only the final dataset (i.e. meeting the selection criteria and having

data available), positive and negative relationships were further separated into their

respective accelerating and decelerating categories.

3.5.1 The influence of scale

The form of the PSRR is often presumed to be scale dependent, with unimodal

relationships being more common at smaller scales and positive relationships being

more common at larger scales (Chase & Leibold, 2002; Waide et al., 1999). Therefore,

the data were examined at two different sampling grains (fine and course) and at three

geographical extents; (continental-to-global, regional and, local-to-landscape). Positive

and negative relationships were again separated into accelerating and decelerating

relationships for each scale examined.

3.5.2 The influence of ecosystem type

The PSRR might be subject to different underlying mechanisms in different ecosystems

types (Waide et al., 1999). Mittelbach et al. (2001) found that the relative frequencies of

different A–PSRRs differed for aquatic and terrestrial ecosystem types. Also, the

surrogates used for productivity vary across different ecosystem types. For example, in

terrestrial systems climatic variables are common, in freshwater aquatic systems

nutrient variables are common, and in marine systems depth is commonly used as a

surrogate for decreasing productivity. Therefore, the data were examined and presented separately for different ecosystem types (i.e. terrestrial, freshwater and marine).

3.5.3 Patterns in homeotherms and poikilotherms

Homeotherms have faster metabolic rates to maintain their constant body temperature. Therefore homeotherms have greater energy requirements than poikilotherms, suggesting that productivity may influence poikilotherms differently to homeotherms. In order to test for any difference between the response of species richness of homeotherms and poikilotherms to differences in productivity, the data were presented separately for poikilotherms and homeotherms.

3.6 Meta-analysis

3.6.1 Calculating effect sizes

A formal meta-analysis relies on effect sizes**.** Effect sizes are first calculated for each study, weighted by sample size and then, using these effect sizes, a grand mean effect size, weighted by the inverse of the sample variance, can be calculated. Therefore, studies with greater replication or less variation in their response have a stronger influence on the grand mean (Cooper et al., 2009; Rosenberg et al., 2000). Given the continuous structure of both the independent and dependent variables, an effect size was calculated from the correlation coefficient. Thus, the coefficients of determination (R^2) for each study were square-root transformed to obtain the correlation coefficient (r).

The correlation coefficients for each member study were then converted to effect sizes using Fisher's *z*-transformation (Hedges & Olkin, 1985):

$$z_r = \frac{1}{2} ln \left(\frac{1 + r}{1 - r} \right)$$

After calculating individual effect sizes for each study, a mean effect size (with a bootstrapped 95% confidence interval) for each relationship type (i.e. positive, negative, unimodal, u-shaped or non-significant) was calculated, weighted by their sampling variance:

$$v_z = \frac{1}{n - 3}$$

When conducting a meta-analysis on regression analyses, all studies must be fitted with the same number of terms (Werenkraut & Ruggiero, 2011). Therefore, given that some studies were linear relationships with a single linear term and others were curvilinear, with both linear and quadratic terms, mean effect sizes (with bootstrapped 95% confidence) were calculated separately for each relationship type. Confidence intervals that include zero indicate that the effect size does not differ significantly from zero. Effect sizes of the different relationships were then compared across the different categories as in *2.3 Vote-count*. Mean effect sizes (with bootstrapped 95% confidence) were also calculated for curvilinear positive and negative relationships. All weighted mean effect sizes were calculated using MetaWin (Rosenberg et al., 2000).

3.6.2 Checking for publication bias

Publication bias is likely to be present in all meta-analyses to some degree. Thus, after comparing the effect size of the different relationships across the various grouping variables (e.g. scales and grains), the data were assessed for the presence of publication

bias. This was first done using a funnel plot (i.e. plotting effect size of each study against sample size) to detect any systematic bias of low effect sizes, particularly studies with non-significant responses, which would suggest the presence of the 'file drawer' problem (see *2.4 Publication bias*) (Greenhouse & Iyengar, 2009). Sample size was log-transformed because there were three studies with particularly large sample sizes which made the plot difficult to examine visually.

4. RESULTS

After excluding studies with small sample sizes (i.e. < 10, n = 82), 387 separate cases from 267 published studies were identified as potential tests of the A–PSRR. This included 88 separate cases from 58 published studies reported in Mittelbach et al. (2001). The form of the A–PSRR could be reasonably identified in 286 cases. After applying the selection criteria, 141 separate cases were accepted as robust tests of the A–PSRR of which 112 (see *Appendix 2* for the studies included in the final analyses) had data available for re-analysis. The most common reason for the rejection of studies was small sample size followed by anthropogenic disturbance of the study system (Table 3). Similar numbers of studies were rejected due to unequal sampling effort/variable area, inappropriate productivity surrogate, data duplication (including those with different data sources but the same taxon over the same geographical location) and unavailable data (Table 3; see *Appendix 1* for detailed rationale for the exclusion of studies from these analyses). Importantly, exclusion is not a criticism of the quality of the studies, but rather they do not fit the criteria for answering the question posed by this research.

4.1 Vote-count

Prior to applying the selection criteria, an exploration of the entire dataset, for which the form of the A–PSRR could be determined (286 cases), indicated that positive relationships were more common in the literature (55.2%) than all other relationships combined (44.7%) (proportion test, $P = 0.007$). Positive relationships were followed by similar proportions of non-significant and unimodal relationships (19.2% and 18.2% respectively) (Figure 5). After applying the selection criteria, the predominance of positive relationships was higher (66.9%) than prior to applying the selection criteria

(Figure 6). Similarly, positive relationships were more common than all other relationships combined (33.1%) (proportion test, $P < 0.0005$). By contrast, the proportion of non-significant (9.4%) and, to a lesser degree unimodal relationships (15.1%), was lower than prior to applying the selection criteria (Figure 6). The main reasons for rejecting non-significant studies included anthropogenic disturbance, variation in area or sampling regime, or a combination of the two (Table 4). After selecting only the 112 cases for which raw data were available, positive relationships were again more common (63.4%) than all other relationships combined (36.6%) (proportion test, $P < 0.0005$) (Figure 7). Again, positive relationships were followed by unimodal (17.9%) and non-significant relationships (8.9%) (Figure 7). Separating the positive and negative relationships into their monotonic, decelerating and accelerating categories revealed that monotonic positive relationships were predominant (33.0%), followed by equal proportions of decelerating positive and unimodal relationships (both 17.9%), and accelerating positive relationships (12.5%) (Figure 8).

Table 3. The number of studies rejected under each selection criterion (see *Appendix 1* for more detailed descriptions of studies not included in the present study)

Criterion	*n*
Unequal sampling effort/variable area	41
Anthropogenic disturbance	56
Introduced species influence	2
Inappropriate productivity surrogate	38
Study design	10
Data duplication	40
Taxonomically restrictive	16
Sample size < 10	82
Data or figure not reported[§]	34
Other[‡]	9

§ Studies that did not report OLS regression or correlation coefficients, or no figure was available to determine the form of the PSR relationship

‡ Includes studies containing a confounding variable or an inappropriate diversity measure (e.g. taxonomically too high)

Table 4. The reasons for excluding non-significant studies from the final vote-count and meta-analysis.

Reason for rejection	*n*
Uneven sampling regime/variable area	10
Anthropogenic influence	4
Inappropriate productivity surrogate	2
Sample size < 10	7
Area varied among sampling sites/anthropogenic influence[§]	15
Other	6

§Both criteria applied to the same study
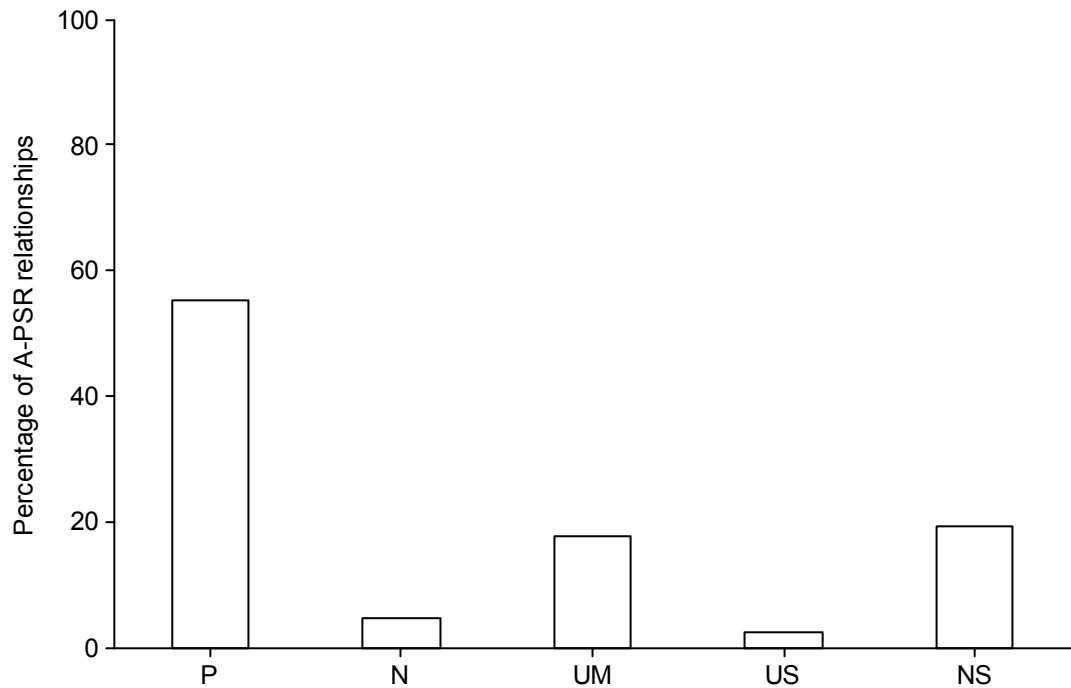
Figure 5. The proportion of different A–PSR (Animal-productivity species richness) relationships within the entire dataset prior to applying any study selection criteria and for which the PSR relationship could be reasonably identified (n = 286). P, positive; N, negative; UM, unimodal; US, u-shaped; NS, non-significant.
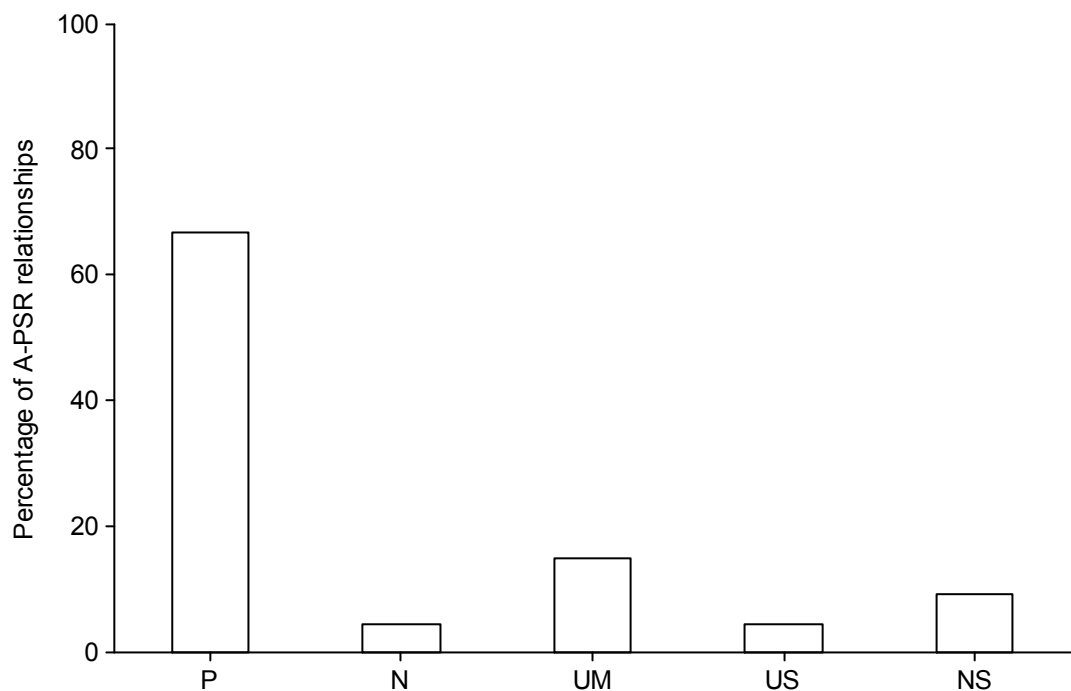
Figure 6. The proportion of different A–PSR relationships after applying the nine selection criteria, including studies for which no raw data were available for re-analysis (n = 141). Relationship codes as in Figure 5.
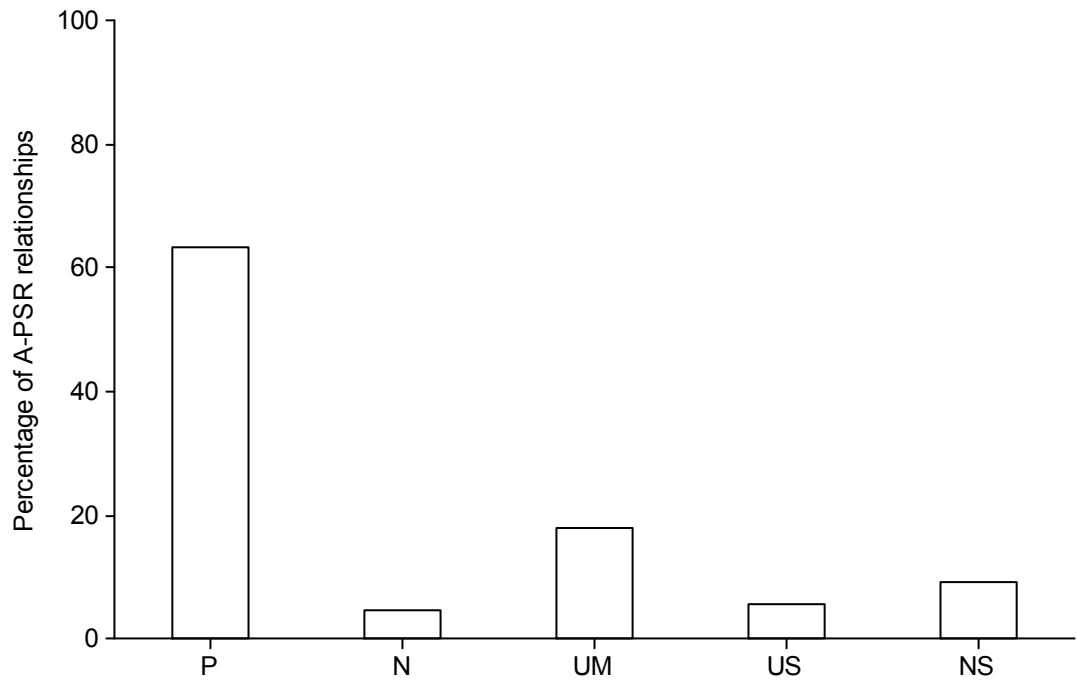
Figure 7. The proportion of different A-PSR studies after applying the nine selection criteria, and for which raw data were available for re-analysis (n = 112). Relationship codes as in Figure 5.
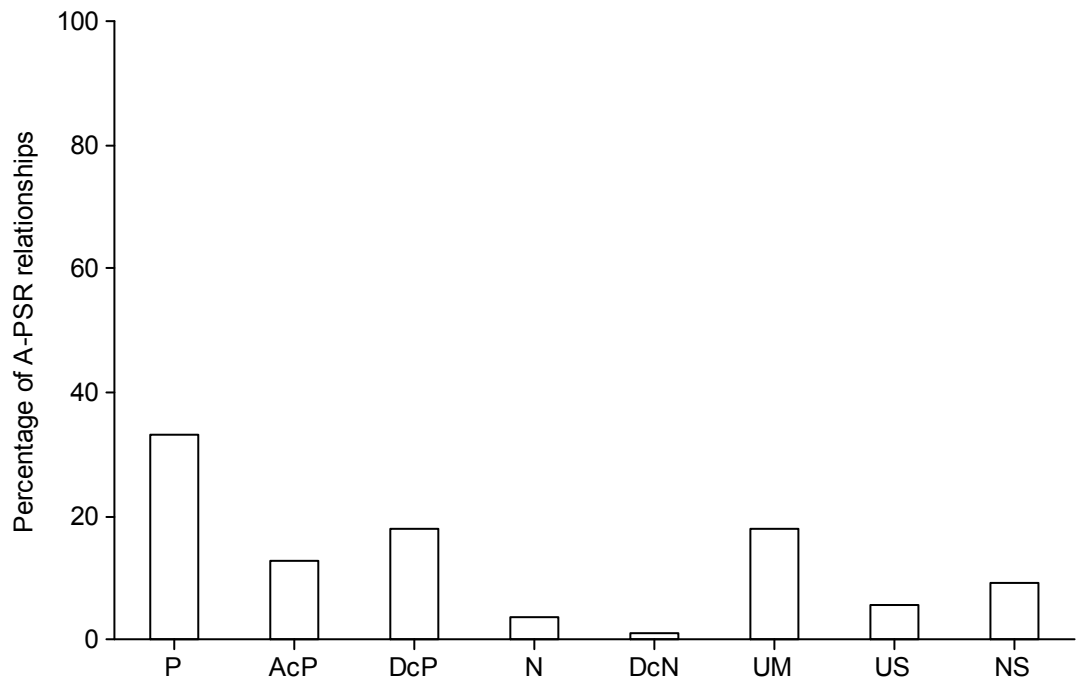
Figure 8. The proportion of different A–PSR relationships, separated into accelerating and decelerating, quadratic relationships for which raw data were available (n = 112). P, positive; AcP, accelerating positive; DcP, decelerating positive; N, negative; DcN, decelerating negative; UM, unimodal; US, u-shaped; NS, non-significant.

4.2 The influence of scale

4.2.1 Geographic extent

The proportions of relationship forms did not differ significantly between geographic extents ($\chi^2 = 13.38$, df $= 8$, $P = 0.099$). Positive A–PSR relationships (i.e. monotonic, accelerating and decelerating combined) were predominant at all three geographic extents (i.e. continental-to-global, regional and local-to-landscape; 86.1%, 58.7% and 56.5% respectively) (Figure 9). At the continental-to-global extent positive relationships (86.1%) were more common than all other relationships combined (i.e. unimodal and u-shaped; 13.9%) (proportion test, $P < 0.0005$). Again, at the regional and local-to-landscape extents positive relationships were more common (58.7% and 56.5% respectively) than all other relationships combined (41.2%, regional; 43.5%, local-to-landscape), but these differences were not statistically significant (proportion test, $P = 0.09$ for regional and $P = 0.372$ for local-to-landscape). Differences between local-to-landscape and regional extents had little influence on the proportions of relationship types (Figure 9).

After separating positive and negative relationships into monotonic, accelerating and decelerating relationships, monotonic relationships were predominant with similar proportions at all three geographical extents (continental-to-global, 36.1%; regional, 37.0%; local-to-landscape, 30.4%) (Figure 10). The proportion of accelerating positive relationships increased with geographic extent. Whereas, the proportions of decelerating positive relationships were similar at continental-to-global and local-to-landscape extents (22.2% and 26.1% respectively) and lower at the regional extent (13.0%). Decelerating negative relationships were only present at the regional extent (2.2%).
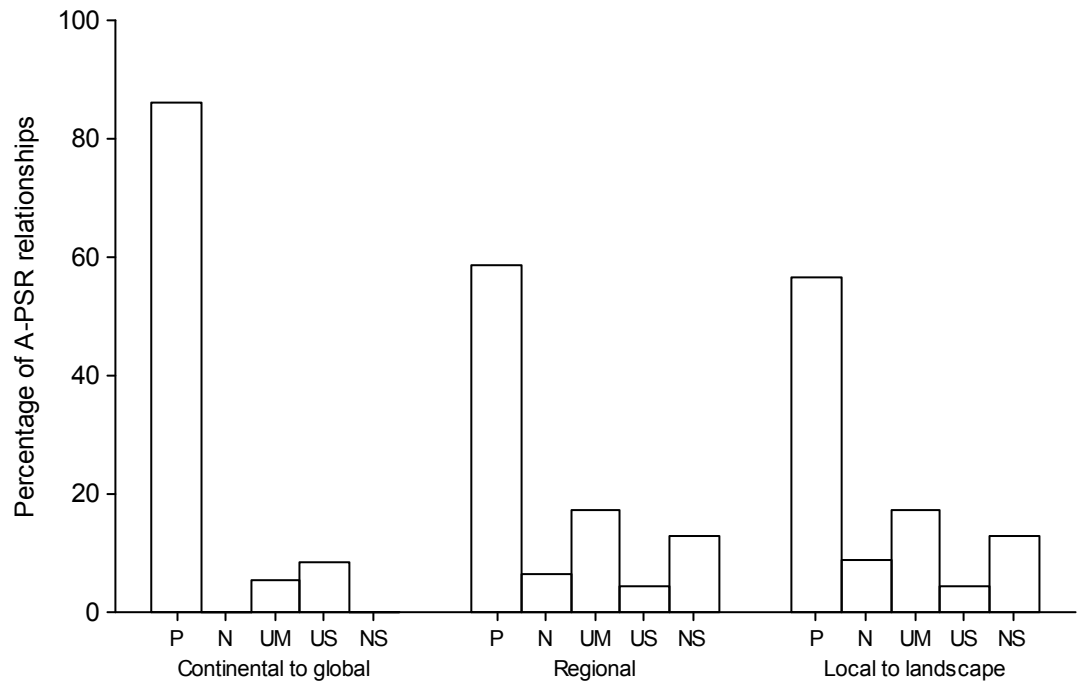
Figure 9. The proportion of different A–PSR relationships at the three geographic scales (continental-to-global, n = 36; Regional, n = 46; Local-to-landscape, n = 23). Relationship codes as in Figure 5.
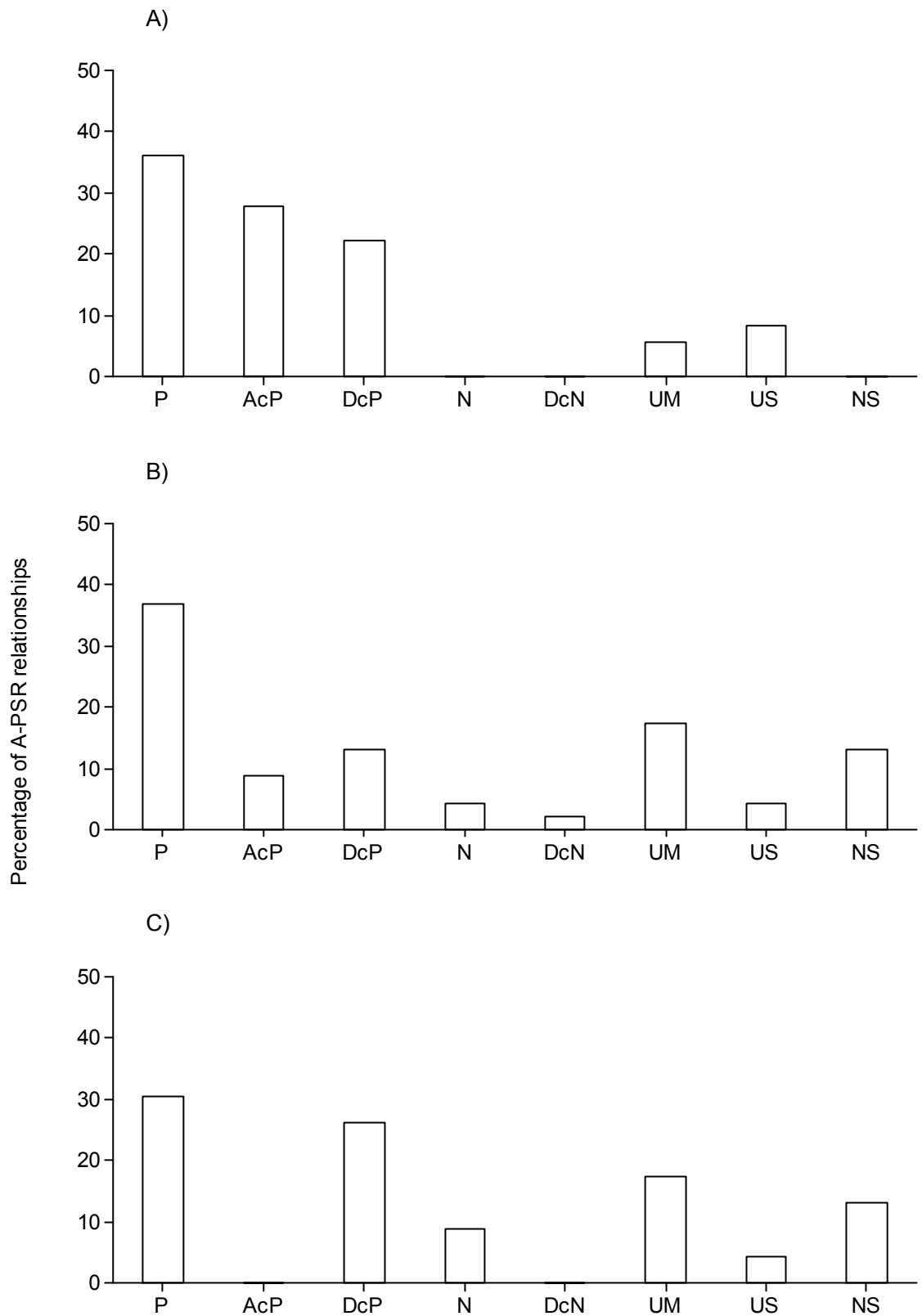
Figure 10. The proportion of different A–PSR relationships at the three spatial extents, separated into their respective accelerating and decelerating, quadratic relationships. (A) Continental-to-global (n = 36); (B) regional (n = 46); (C) local-to-landscape (n = 23). Relationship codes as in Figure 8.

4.2.2 Grain

The proportions of relationship forms differed according to the sampling grains employed, but the difference was marginally non-significant ($\chi^2 = 8.60$, df $= 4$, $P = 0.072$). At both the coarse and fine grain, positive relationships were predominant (73.9% and 50.0% respectively) (Figure 11) and, at the coarse grain positive relationships were more common than all other relationships combined (proportion test, $P < 0.0005$). Unimodal relationships were the second most common at both fine and coarse grains (23.3% and 8.7% respectively).

After separating the positive and negative relationships into accelerating and decelerating, quadratic relationships, positive monotonic relationships predominate at both the coarse (34.8%) and fine (33.3%) sampling grains with similar proportions (Figure 12 and 13), but there were greater proportions of accelerating and decelerating positive relationships from coarse grain studies than from fine grain studies.
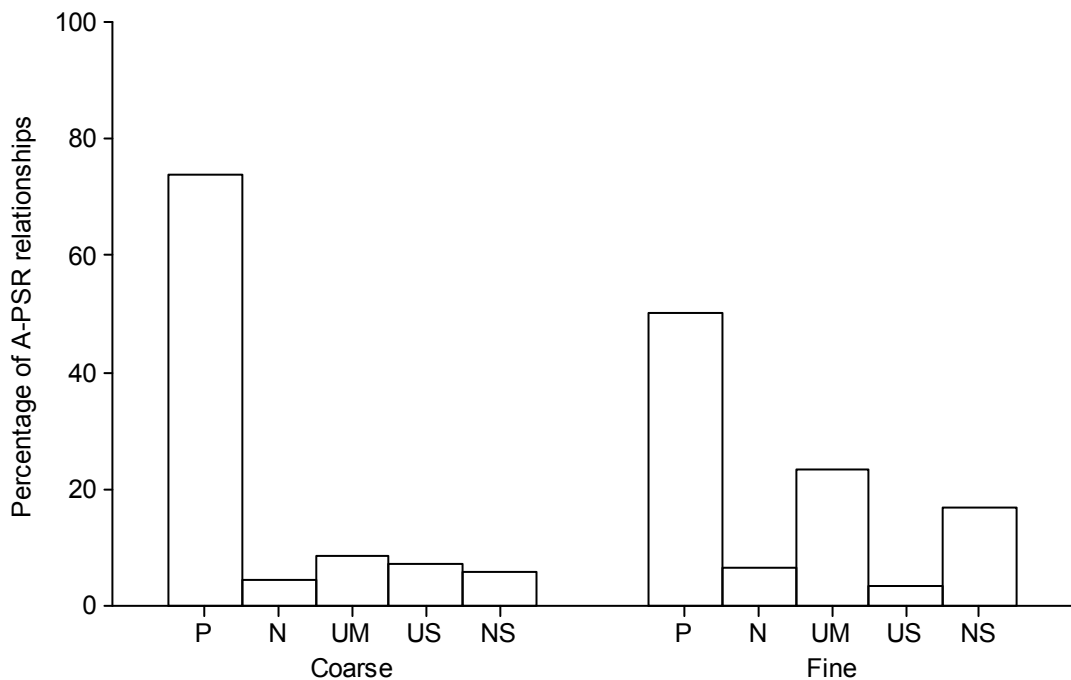
Figure 11. The proportion of different A–PSR relationships at the two sampling grains (coarse, n = 69; fine, n = 29). Relationship codes as in Figure 5.
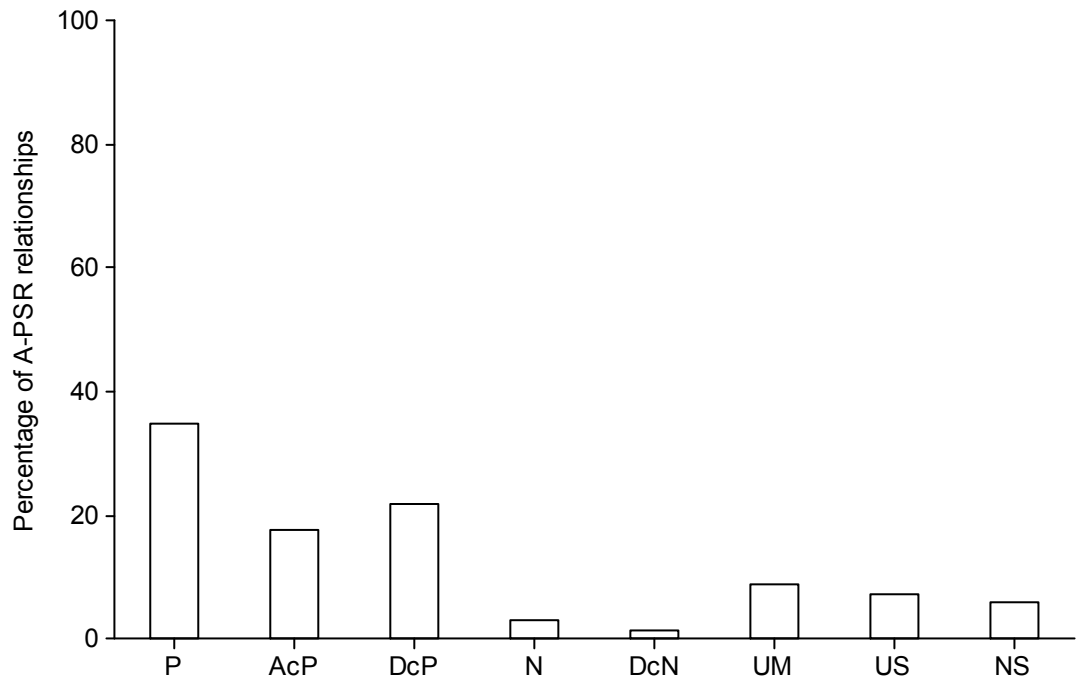
Figure 12. The proportion of different A–PSR relationships at the coarse sampling grain, separated into their respective accelerating and decelerating, quadratic relationships (n = 69). Relationship codes as in Figure 8.
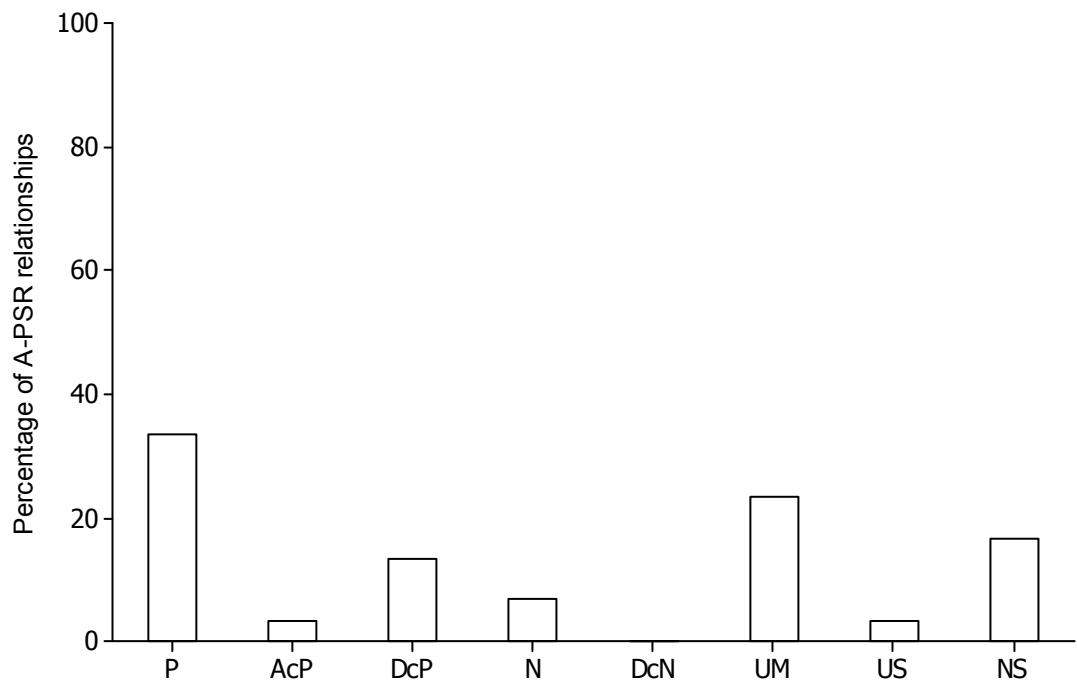
Figure 13. The proportion of different A–PSR relationships at the fine sampling grain, separated into their respective accelerating and decelerating, quadratic relationships (n = 29). Relationship codes as in Figure 8.

4.3 The influence of ecosystem type

Positive relationships predominated in studies within terrestrial and freshwater aquatic ecosystems, whereas unimodal relationships predominated within marine ecosystems (42.9%) (Figure 14). Additionally, in terrestrial ecosystems, positive relationships were more common than all other relationships combined (proportion test, $P < 0.0005$). Unimodal relationships were also more common in freshwater aquatic systems than in terrestrial systems.

After separating the positive and negative relationships into accelerating and decelerating relationships, positive monotonic relationships were predominant in terrestrial systems (42.6%) (Figure 15A) and unimodal relationships were predominant in marine systems (42.9%) (Figure 15C). However, in freshwater aquatic systems, positive monotonic (26.1%), decelerating positive (21.7%) and unimodal (21.7%) relationships occurred in similar proportions (Figure 15B).
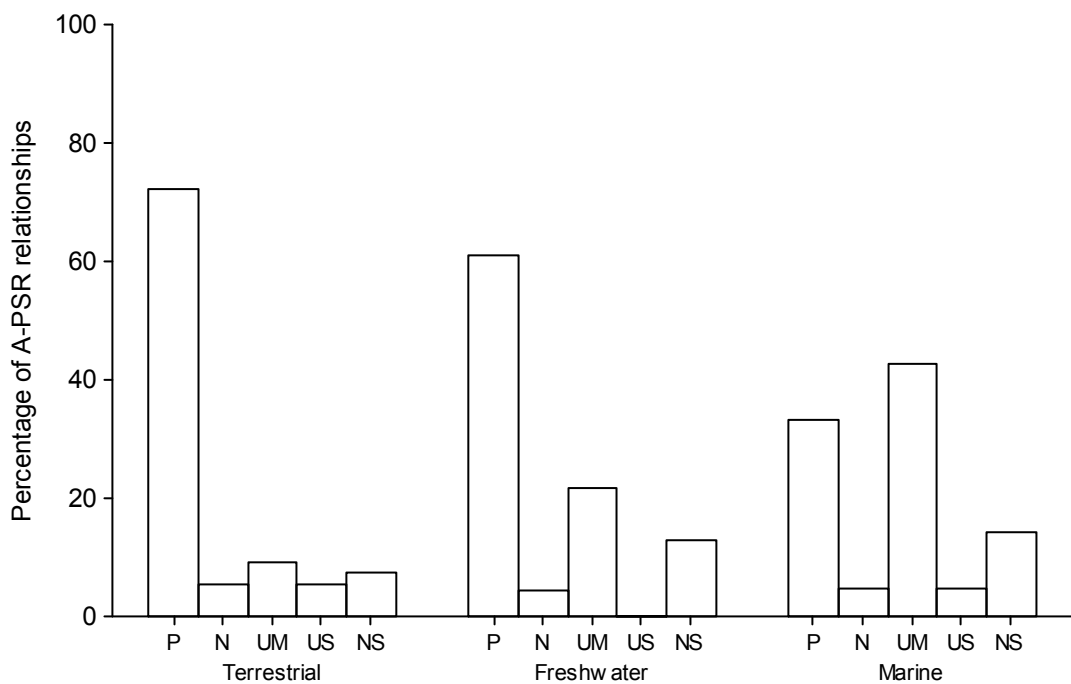
Figure 14. The proportion of different A–PSR relationships in different ecosystem types (terrestrial, n = 54; freshwater, n = 23; marine, n = 21). Relationship codes as in Figure 5.
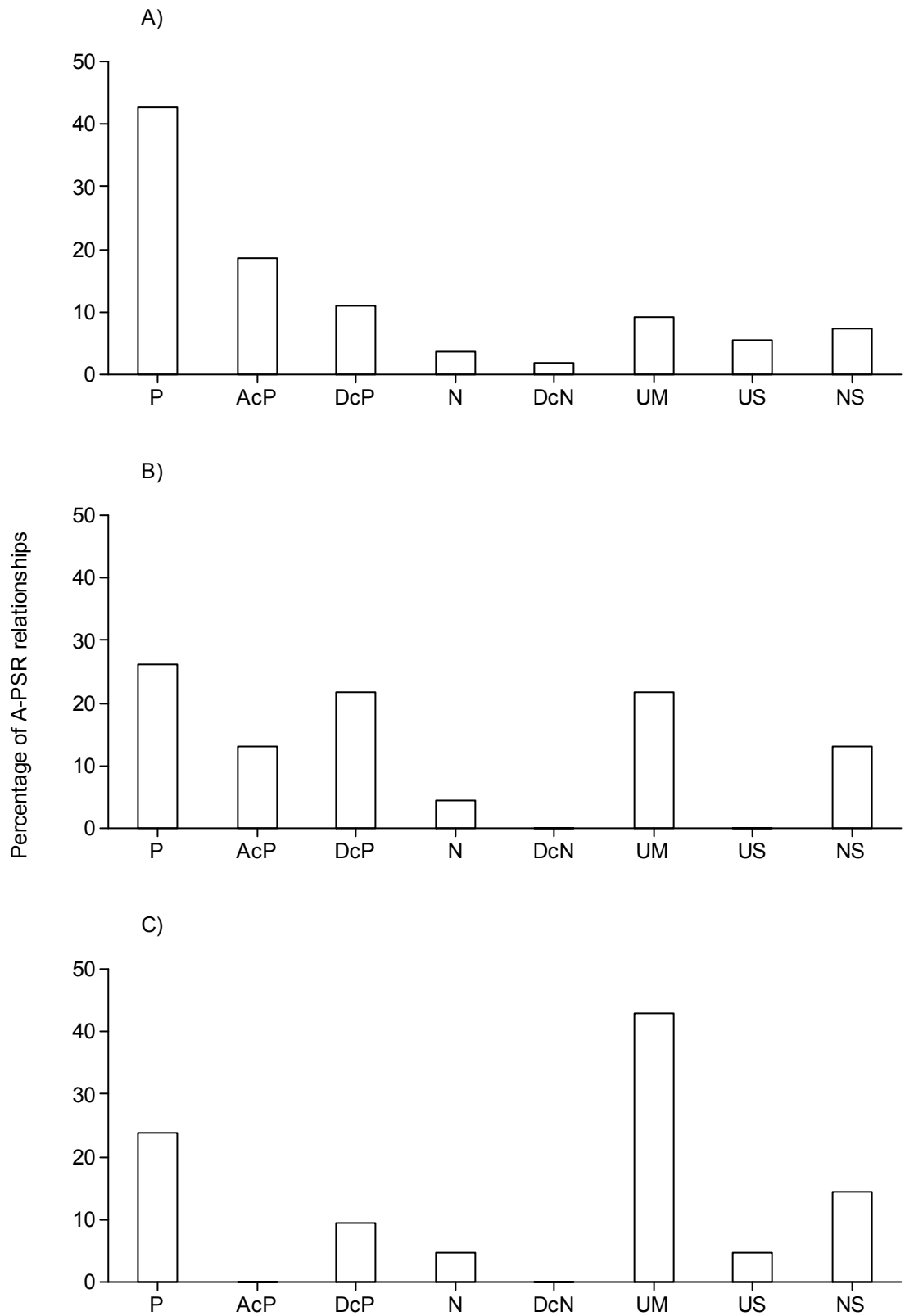
Figure 15. The proportion of different A–PSR relationships in different ecosystems, separated into their respective accelerating and decelerating, quadratic relationships. (A) Terrestrial (n = 54); (B) freshwater (n = 23); (C) marine (n = 21). Relationship codes as in Figure 8.

4.4 Patterns in homeotherms and poikilotherms

There was no statistical difference in the proportions of different forms of the A–PSRR relationship in homeo- and poikilotherms ($\chi^2 = 4.33$, df $= 4$, $P = 0.363$). Positive A–PSRRs were predominant in both poikilo- and homeotherms (57.7% and 76.5% respectively) (Figure 16) and in homeotherms, positive A–PSRRs were more common than all other relationships combined (23.5%) (proportion test, $P < 0.0005$). There were more unimodal relationships among poikilotherms (21.8%) than homeotherms (8.8%). After separating positive and negative relationships in accelerating and decelerating forms, positive monotonic A–PSRRs were predominant for both poikilo- and homeotherms (32.1% and 35.3% respectively) (Figure 17 and 18). For poikilotherms there were equal proportions of accelerating and decelerating positive relationships (12.8%), but in homeotherms there were more decelerating positives (29.4%) than accelerating positives (11.8%).
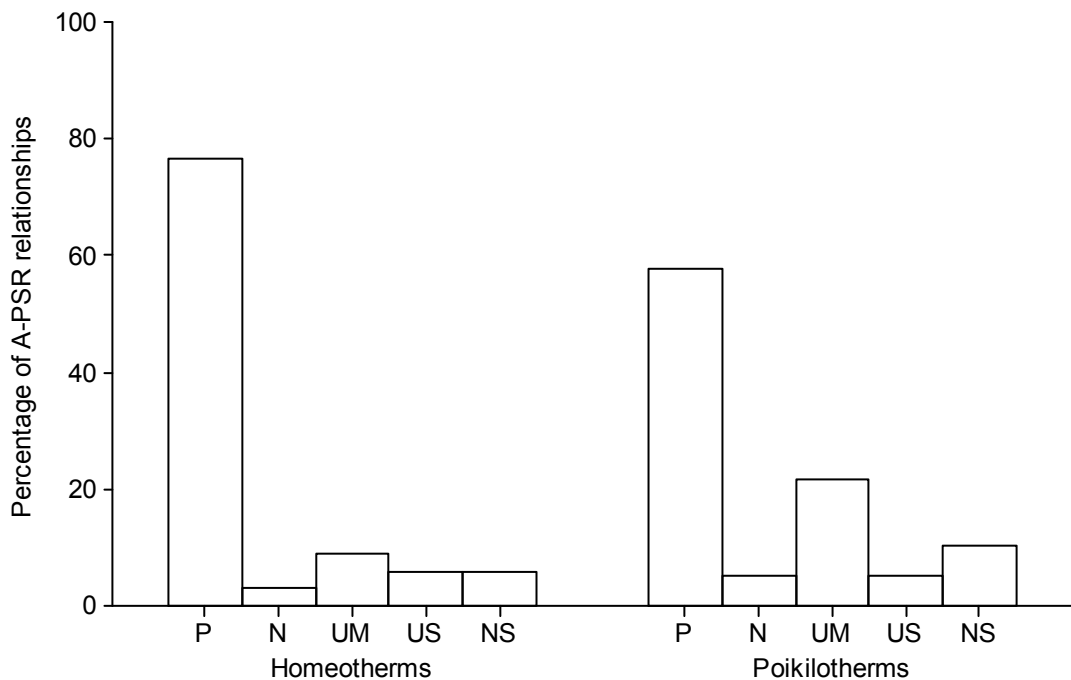
Figure 16. The proportion of different A–PSR relationships in homeotherms and poikilotherms (homeotherms, n = 34; poikilotherms n = 78). Relationship codes as in Figure 5.
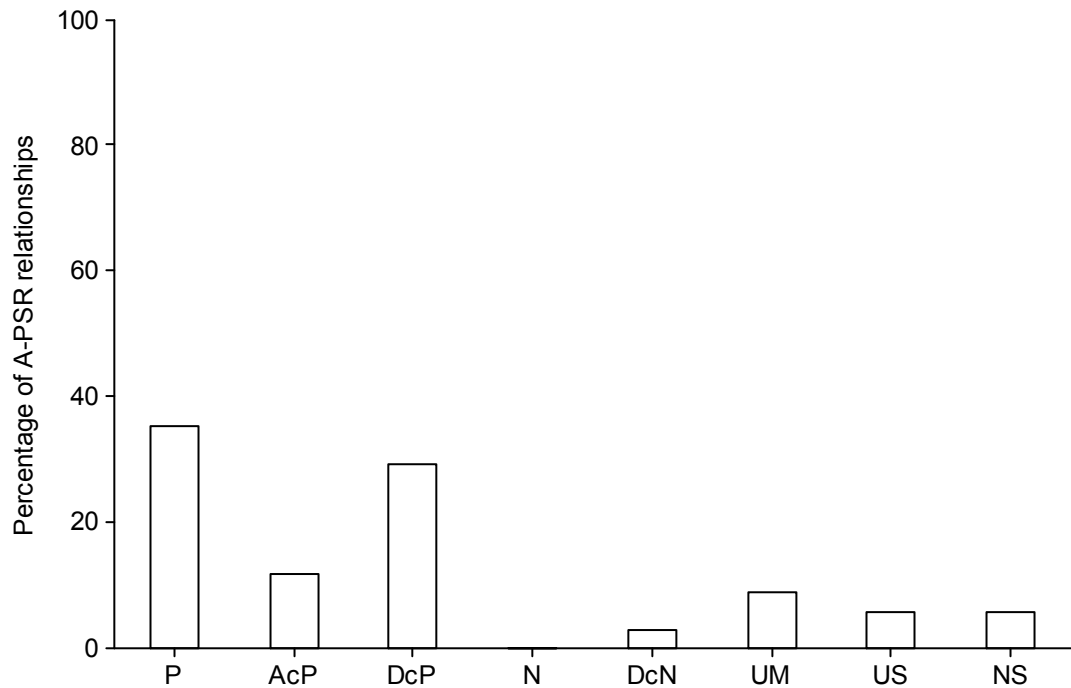
Figure 17. The proportion of different A–PSR relationships in homeotherms, separated into their respective accelerating and decelerating, quadratic relationships (n = 34). Relationship codes as in Figure 8.
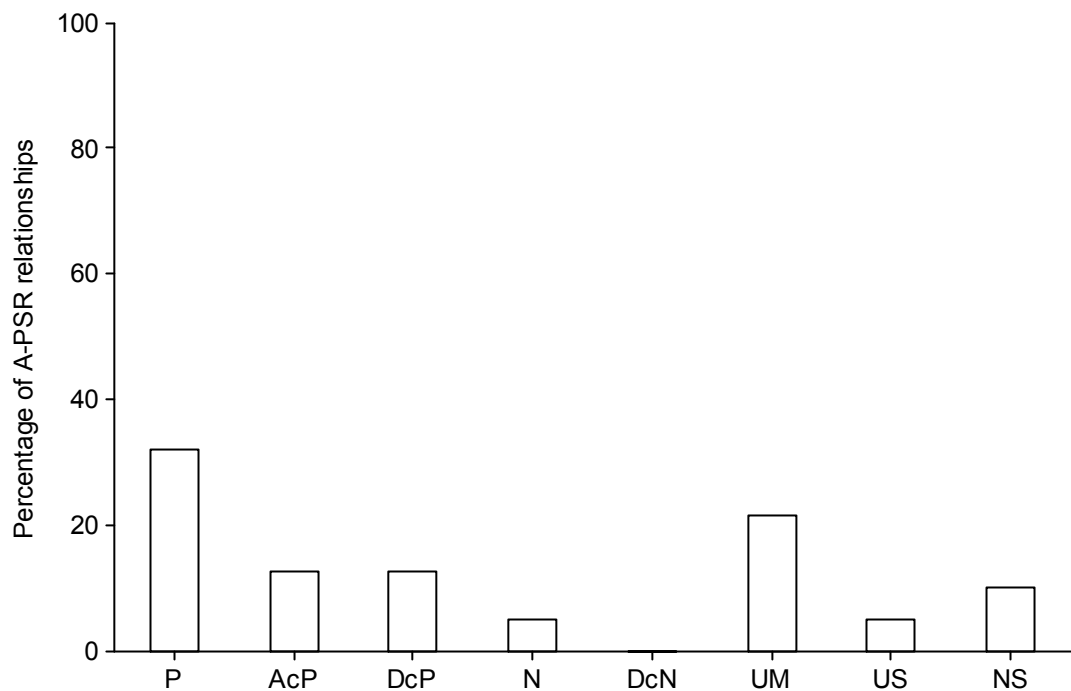
Figure 18. The proportion of different A–PSR relationships in poikilothermic organisms, separated into their respective accelerating and decelerating, quadratic relationships (n = 78). Relationship codes as in Figure 8.

4.5 Meta-analysis

Across the whole dataset positive and negative relationships had the highest effect size (0.9737 and 0.9324 respectively) followed by unimodal and u-shaped relationships (0.7216 and 0.6512 respectively) (Figure 19). The wide confidence interval of the negative relationships reflects the low frequency at which they occurred (4.5%) (see Figure 7).

When separating positive and negative relationships into accelerating and decelerating relationships, accelerating positive relationships had the highest mean effect size (1.1203) followed by negative (0.9443), monotonic positive (0.9269) and decelerating positive (0.9256) relationships (Figure 20). No mean effect size could be calculated for decelerating negative relationships since there was only a single decelerating negative relationship (Rosenberg et al., 2000) present in the dataset. Furthermore, accelerating positive relationships had higher effect sizes (with non-overlapping confidence intervals) than unimodal, u-shaped and non-significant relationships.
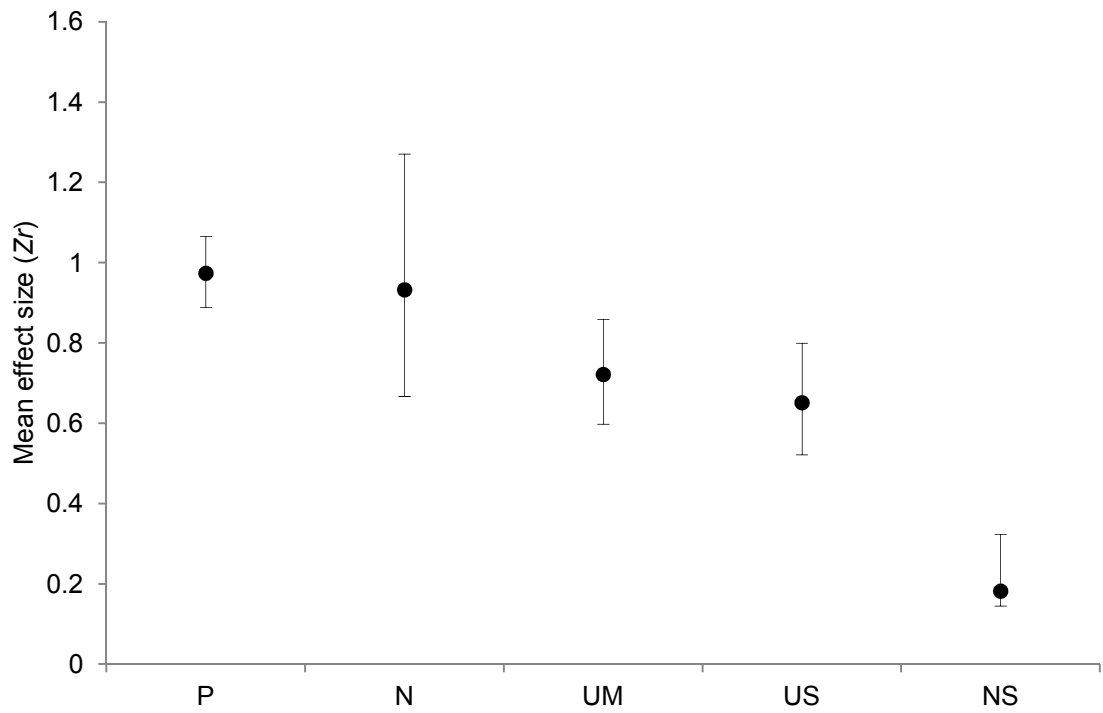
Figure 19. Mean effect sizes (with 95% confidence intervals) of different A–PSR relationships (n = 112). Relationship codes as in Figure 5.
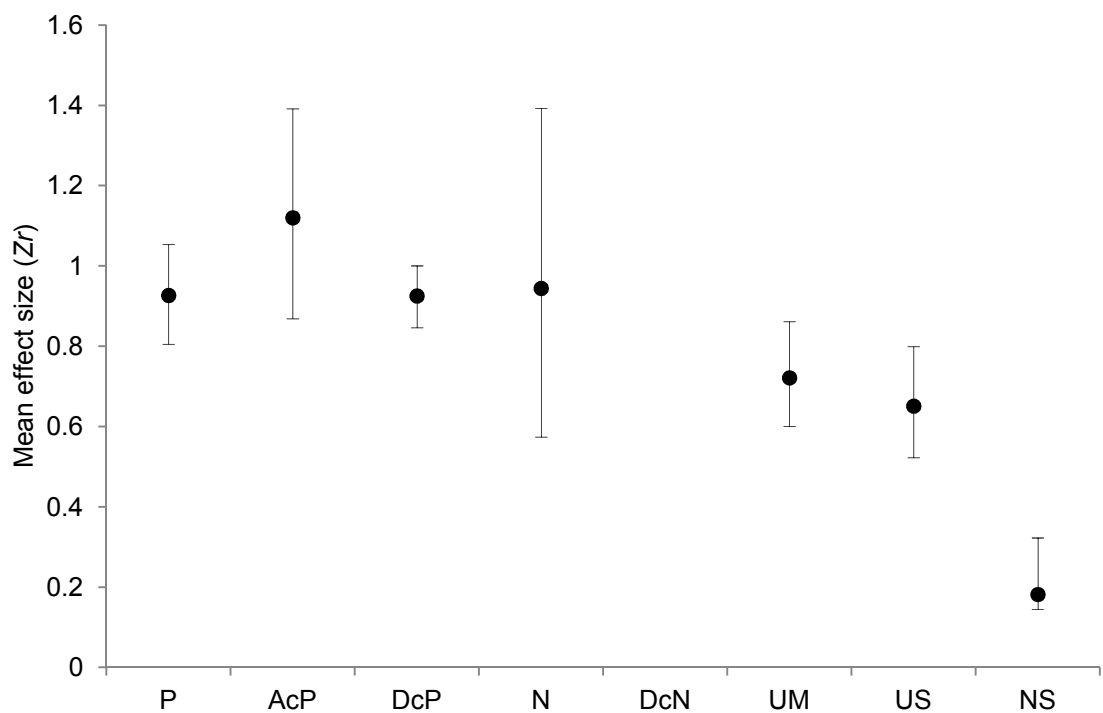
Figure 20. Mean effect sizes(with 95% confidence intervals) of different A–PSR relationships, separated into their respective accelerating and decelerating, quadratic relationships (n = 111). Relationship codes as in Figure 5.

4.6 Effect sizes across scales

4.6.1 Geographic extent

Positive relationships had the highest effect size at the continental-to-global (1.0266) and the local-to-landscape (1.0215) extents and negative relationships had the highest effect size at the regional extent (0.8871) (Figure 21). At the continental-to-global scale positive relationships had a higher mean effect size (with non-overlapping confidence intervals) than u-shaped relationships. At the regional and landscape scales there was no clear differences in effect size among the different relationship types except that, as would be expected by their intrinsic nature, non-significant relationships had low effect sizes. Positive relationships had the second highest mean effect size at the regional scale (0.8802) with a narrower confidence interval than negative relationships, reflecting the greater frequency at which they occurred relative to negative relationships (see Figure 9). At the local-to-landscape scale positive relationships had a higher mean effect size (with non-overlapping confidence intervals) than unimodal relationships. In addition, the wide levels of confidence around negative relationships at the local-to-landscape scale reflect their relatively low frequency (see Figure 9). No mean effect sizes could be calculated for negative and non-significant relationships at the continental scale or, u-shaped relationships at the local-to-landscape scale because only a single relationship (Rosenberg et al., 2000) occurred at the respective scales.
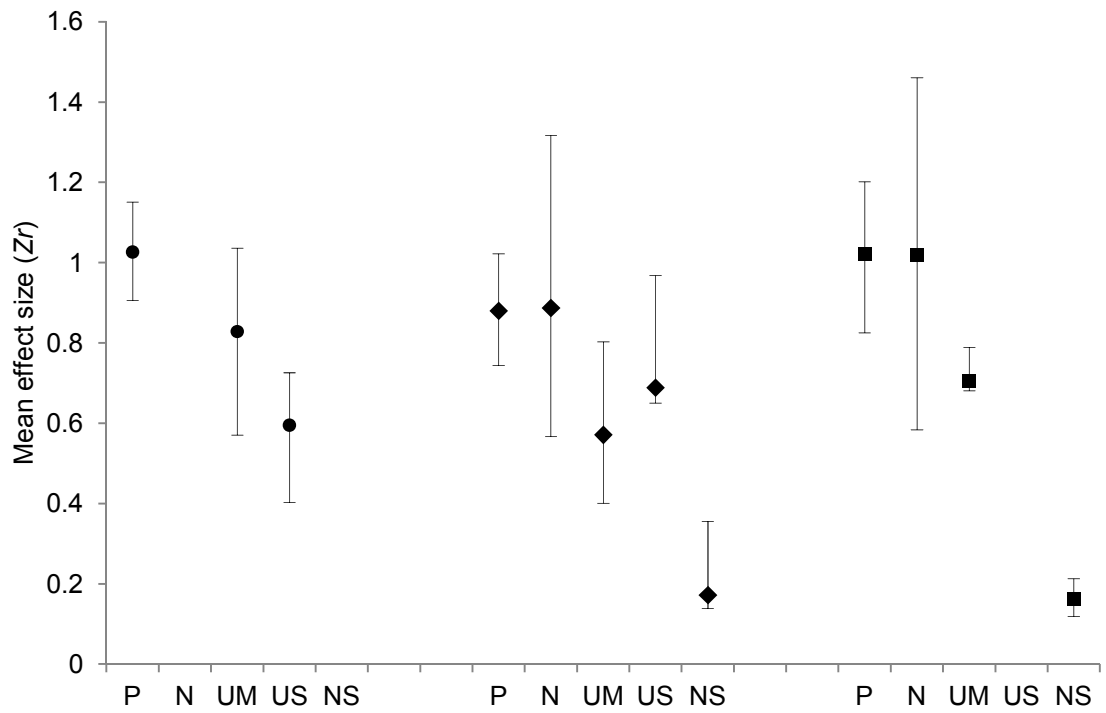
Figure 21. The mean effect sizes (with 95% confidence intervals) of different A–PSR relationships across different geographical scales (●, continental-to-global, n = 36; ♦, regional, n = 46; ■, local-to-landscape, n = 22). Relationship codes as in Figure 5.

4.6.2 Grain

At the coarse grain, positive relationships had the highest mean effect size (0.9914), whereas at the fine grain negative relationships had highest mean effect size (1.4012) (Figure 22). Importantly however, there were only two negative relationships recorded at the fine grain relative to 15 positive relationships (see Figure 11). At the coarse sampling grain, positive relationships had a higher mean effect size (with non-overlapping confidence intervals) than unimodal, and u-shaped relationships. At the fine grain, non-significant relationships had significantly lower effect size than all other relationships. However, there was only a single u-shaped relationship at the fine grain making calculation of a mean effect size impossible (Rosenberg et al., 2000).
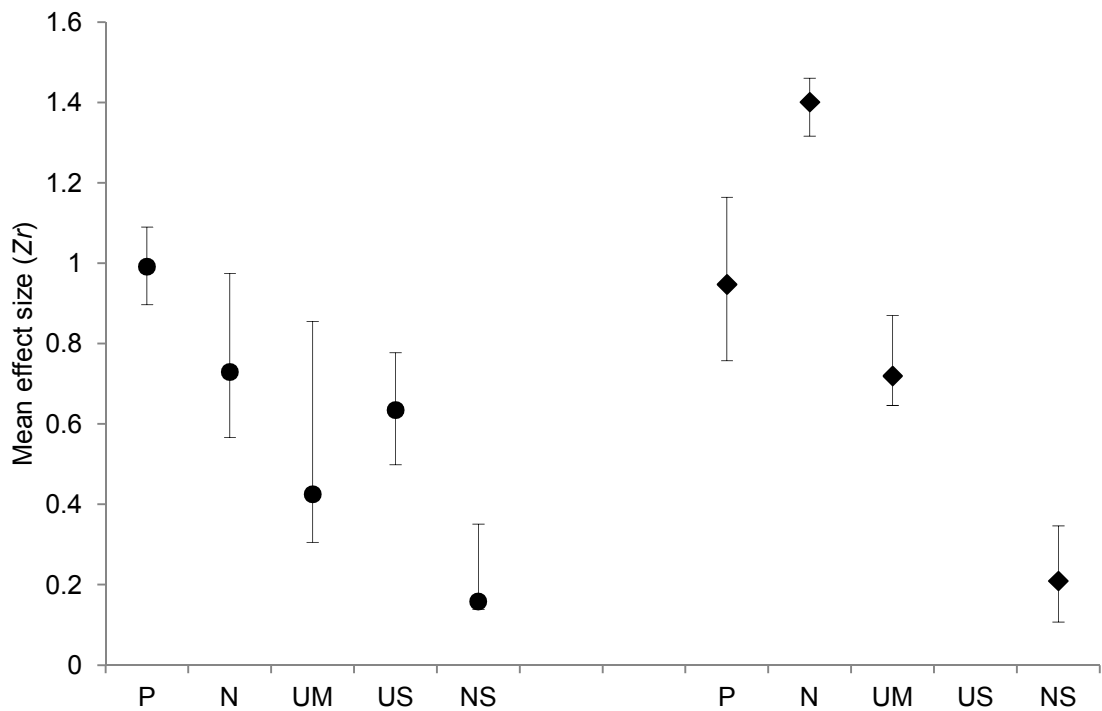
Figure 22. The mean effect sizes (with 95% confidence intervals) of different A–PSR relationships at different sampling grains (●, coarse, n = 69; ♦, fine, n = 28). Relationship codes as in Figure 5.

4.7 Effect size across different ecosystem types

Mean effect sizes were highest for positive relationship forms in terrestrial (1.0426) and freshwater aquatic (0.8877) systems, whereas unimodal relationships had the highest effect size in marine systems (0.8370) (Figure 23). In terrestrial ecosystems, positive relationships had a higher mean effect size (with non-overlapping confidence intervals) than unimodal relationships (0.4764).
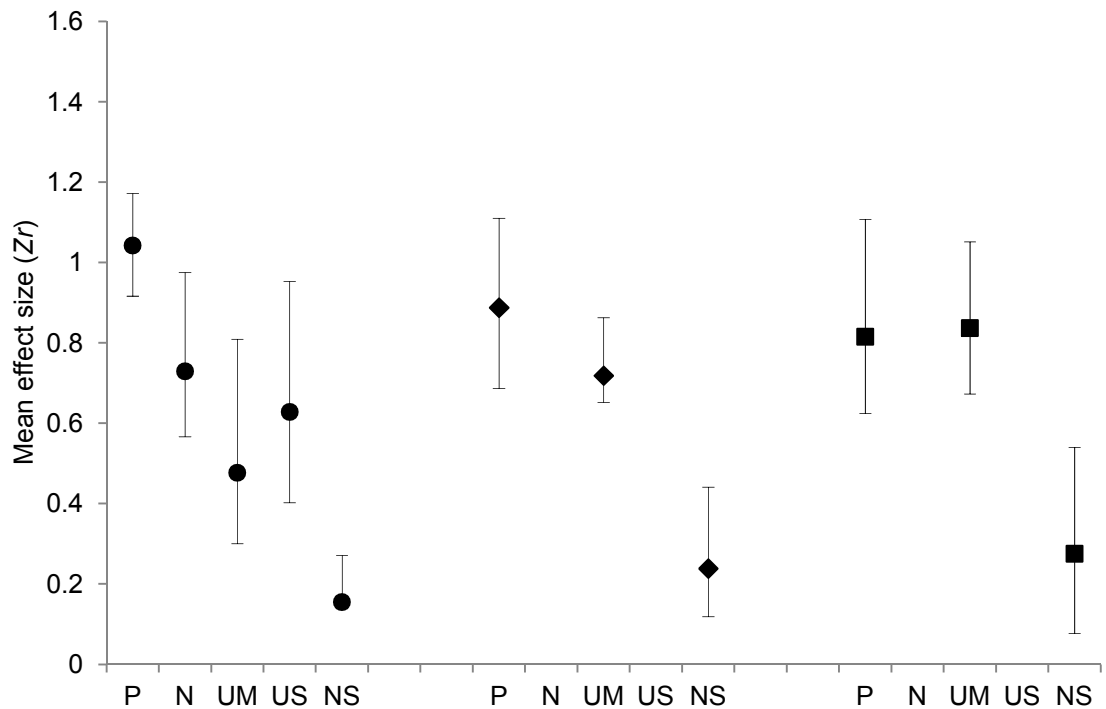
Figure 23. The mean effect sizes (with 95% confidence intervals) of different A–PSR relationships across different ecosystem types (●, terrestrial, n = 54; ♦, freshwater, n = 22; ■, marine, n = 19). Relationship codes as in Figure 5.

4.8 Effect sizes in homeotherms and poikilotherms

Positive relationships had the highest effect size in both homeotherms (0.9860) and poikilotherms (0.9648) (Figure 24). Furthermore, in poikilotherms, positive relationships had a significantly higher mean effect size (with non-overlapping confidence intervals) than u-shaped relationships.
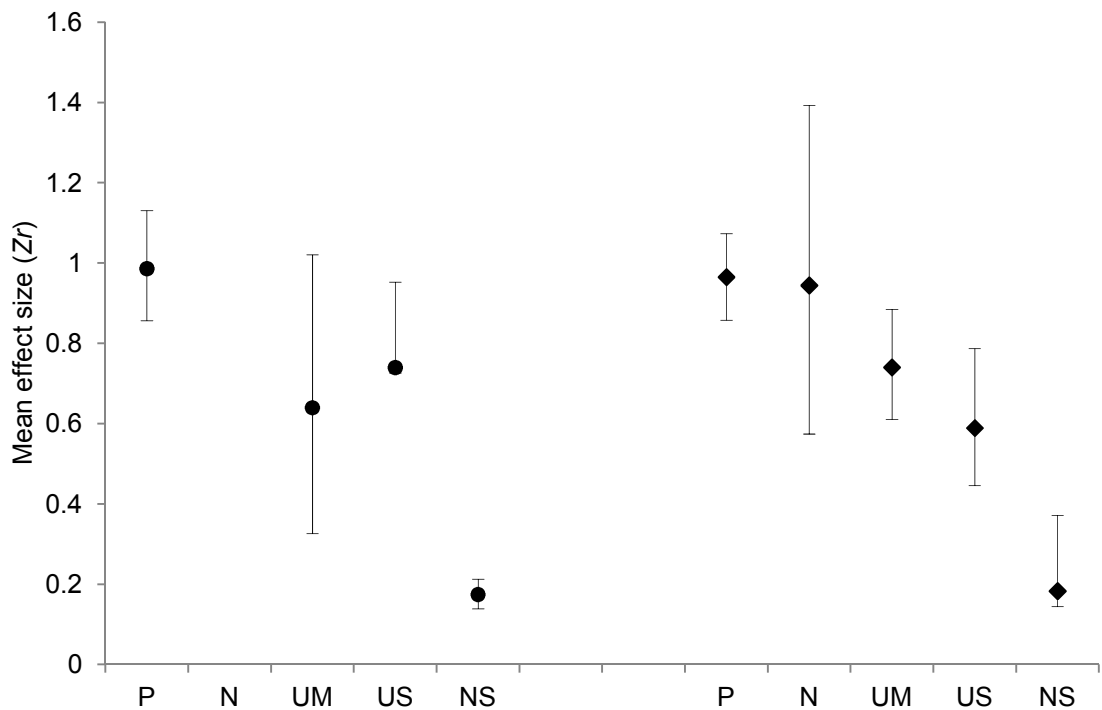
Figure 24. The mean effect sizes (with 95% confidence intervals) of different A–PSR relationships of homeotherms and poikilotherms (●, homeotherms, n = 33; ♦, poikilotherms, n = 78). Relationship codes as in Figure 5.

4.9 Assessing publication bias

There is no clear systematic bias against studies with low effect size with corresponding low sample sizes (Figure 25). Studies at the low end of the effect size spectrum also tend to have low sample size suggesting that the influence of the 'file drawer' problem is minimal (i.e. there was little evidence of systematic bias against studies with non-significant results).
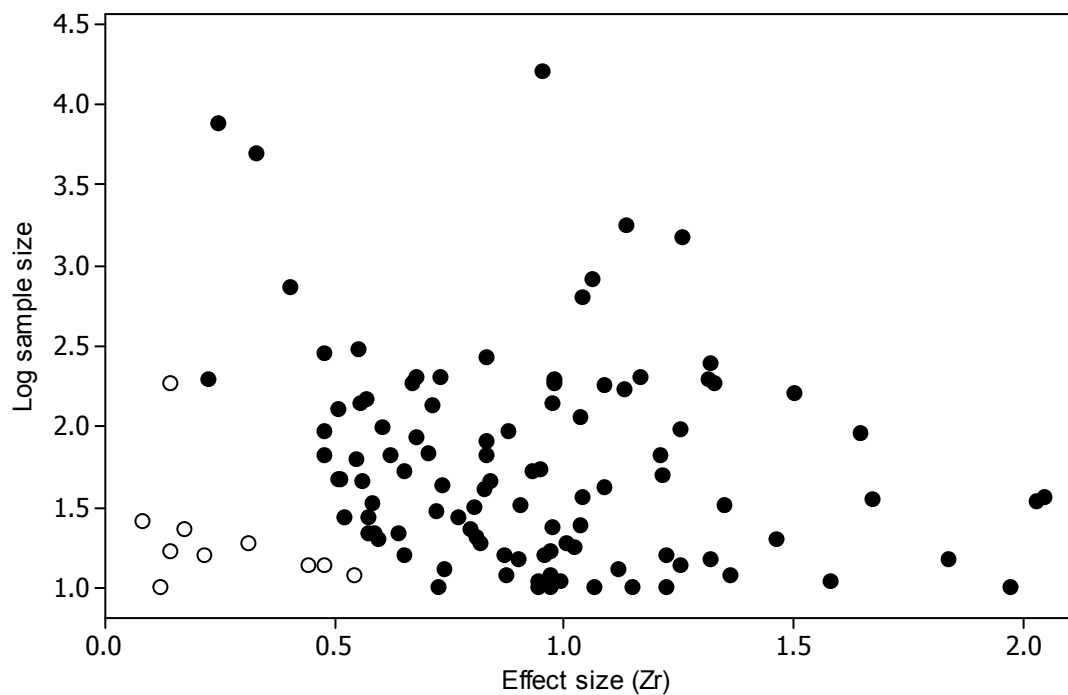
Figure 25. A funnel plot effect size plotted against sample size (log transformed) (n = 112). (●, studies with significant relationships; ○, studies with non-significant relationships)

5. DISCUSSION

Positive A–PSRRs were found to predominate in the present study. These results contrast substantially with those of the previous review by Mittelbach et al. (2001). Across their whole dataset Mittelbach et al. (2001) found that unimodal relationships were the most common form of the A–PSRR. Within geographical scales (i.e. local-to-landscape, regional and continental-to-global) they found negative, positive and unimodal relationships were common with no one relationship predominating (Figure 26). However, in the present study, positive relationships were the most common form across the whole dataset. Furthermore, at the continental-to-global (> 4000km) extent positive relationships were more common than all other relationships combined. At regional (200–4000km) and local-to-landscape (< 200km) extents positive relationships were predominant although unimodal relationships were more common than at the largest extent (Figure 27). Mittelbach et al. (2001) reported that unimodal relationships were common in aquatic systems (Figure 28) although freshwater and marine systems were not analysed separately. In the present study marine and freshwater studies were analysed separately. The proportion of unimodal relationships was higher in freshwater than terrestrial systems, and unimodal relationships were the most common form of the A–PSRR in marine studies. However, when freshwater and marine studies in the present study are combined into a single category, positive relationships remain the most common form of the A–PSRR (Figure 29). Explanations for these contrasts are discussed in detail below (*5.3 Explaining the contrast with Mittelbach et al (2001)*).
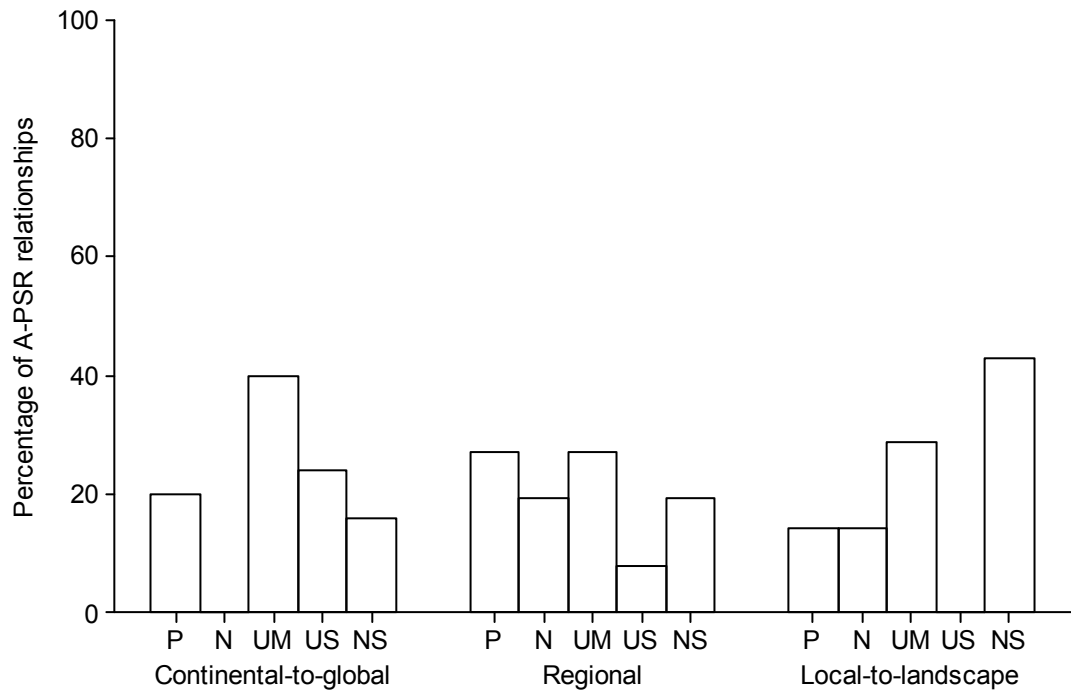
Figure 26. The proportions of different A–PSR relationships across geographical extents reported by Mittelbach et al. (2001) (continental-to-global, N = 25; regional, N = 26, local-to-landscape, N = 14). Relationship codes as in Figure 5.
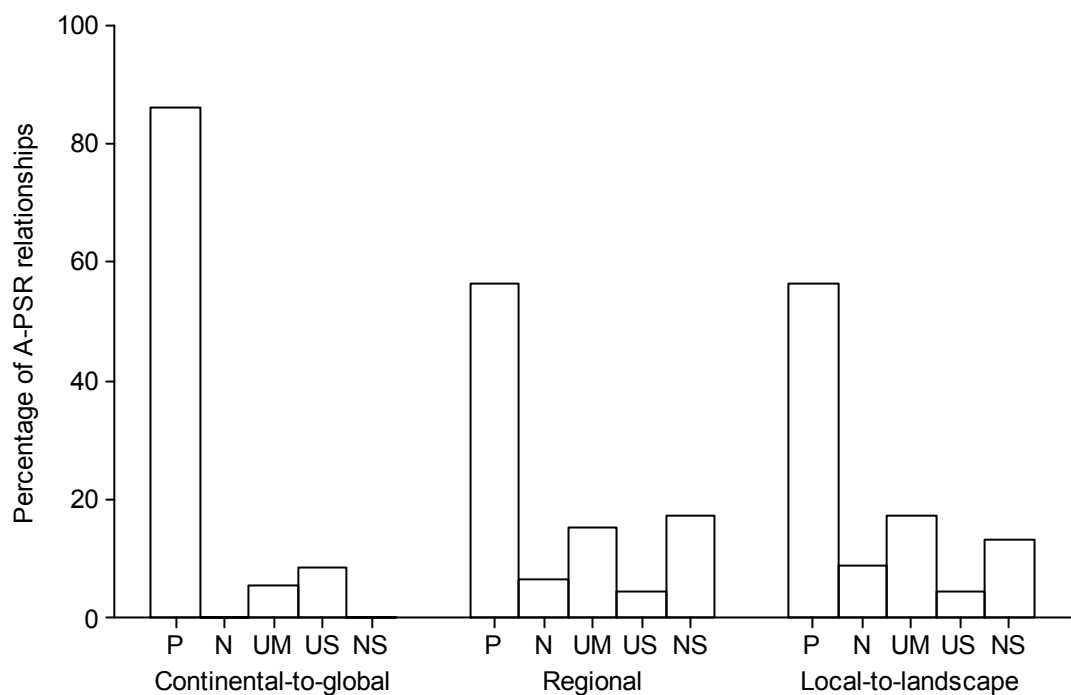
Figure 27. The proportion of different A–PSR relationships at the three geographic extents reported in the present study (continental-to-global, N = 36; Regional, N = 46; Local-to-landscape, N = 23). Relationship codes as in Figure 5.
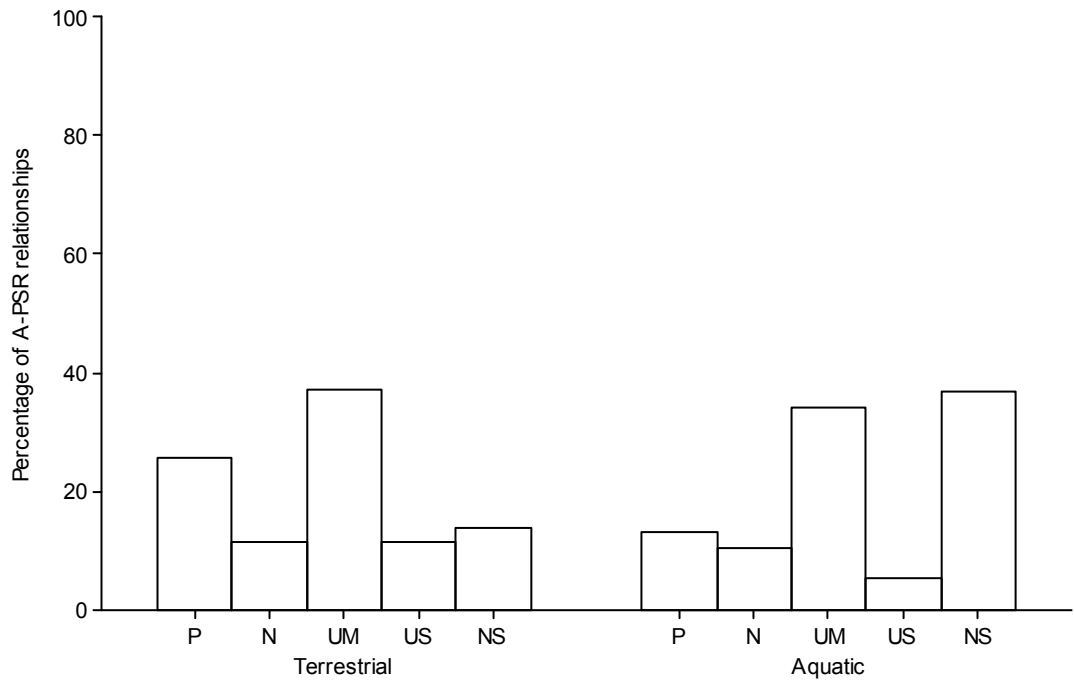
Figure 28. The proportion of different A–PSR relationships in different ecosystem types reported by Mittelbach et al. (2001) (terrestrial, N = 43; aquatic N = 38). Relationship codes as in Figure 5.
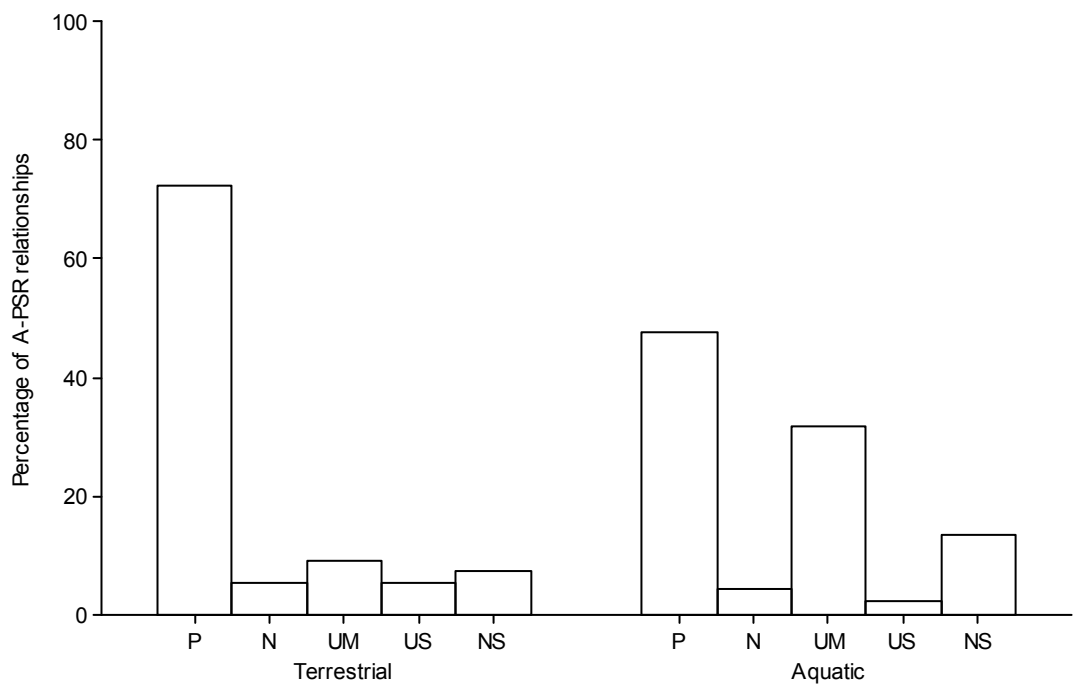
Figure 29. The proportion of different A–PSR relationships in different ecosystem types reported in the present study (terrestrial, N = 54; aquatic N = 44). Relationship codes as in Figure 5.

5.1 A note on negative and u-shaped relationships

Negative and u-shaped relationships were rare across the whole dataset. This is a general observation in the literature (Gillman & Wright, 2006; Rosenzweig & Abramsky, 1993). Negative relationships lack a general theoretical explanation; Rosenzweig and Abramsky (1993) argue that negative relationships only represent the declining phase of a unimodal relationship. Pärtel et al. (2007) combined negative relationships and unimodal relationships following this reasoning. Similarly, u-shaped relationships have few general explanations. However, they are explainable in some cases. Scheiner and Jones (2002) suggest that transitional zones between communities (i.e. ecotones) at low productivity might elevate species richness in these areas resulting in an apparent u-shape. U-shaped relationships can also be explained by the species pool hypothesis. If mid-productivity sites are rare then the species pool for these sites is likely to be low. Therefore, the alpha diversity in mid-productivity sites would be low because of a small species pool for these sites (Gillman & Wright, 2006). Nonetheless, Pärtel et al. (2007) collapsed u-shape relationships into non-significant relationships, on the basis that they have no theoretical explanation However, reclassifying negative and u-shaped relationships found in the present study as unimodal and non-significant relationships respectively only involved 11 studies. Moreover, this had little effect on the overall pattern; positive relationships remained more common than unimodal and non-significant relationships combined (proportion test, $P < 0.0005$) (Figure 30).
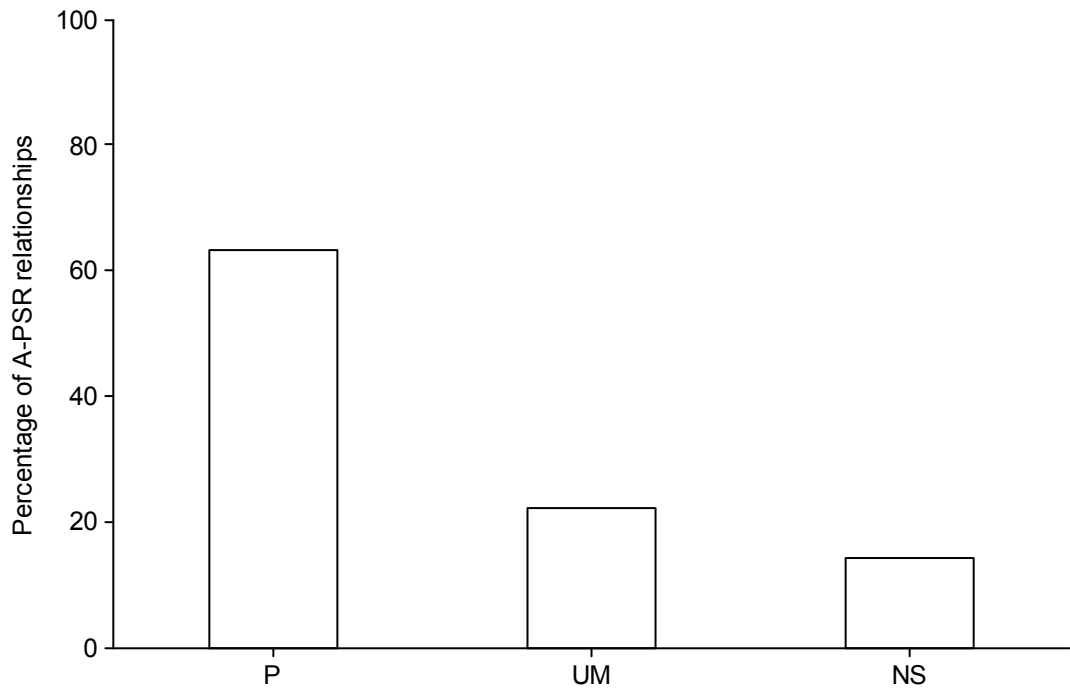
Figure 30. The proportion of different A–PSR relationships after collapsing negative into unimodal relationships, and collapsing u-shaped into non-significant relationships (N = 112). Relationship codes as in Figure 5.

5.2 Dataset description

The low proportion of studies (~33%) accepted for the vote-count and subsequent meta-analysis highlights two important points for literature synthesis. Firstly, the large number of studies excluded from the final analyses after applying the selection criteria suggests that carefully scrutinising each potential member study for appropriateness in answering the research question is crucial. Secondly, the 28 studies for which data were not available suggests greater data availability is needed for ecological publications. Twenty-six of these studies were published since 2000. The availability of data from recent publications is of some concern especially given the increasing usage of meta-analyses and research syntheses in ecology. However, with respect to this study, the first point is more important given that applying the selection criteria eliminated many more

studies (206 separate cases) than a lack of data did. However, a lack of data did prevent the calculation of effect sizes for meta-analysis.

These conclusions are consistent with the research synthesis literature (see *2.3 Study selection*), and specifically the forum in *Ecology* on meta-analysis and the plant–PSRR (e.g. Gillman & Wright, 2010; Gurevitch & Mengersen, 2010; Hillebrand & Cardinale, 2010; Whittaker, 2010b). However, opinions differ on the stringency, application and specific criteria that should be applied. The criteria proposed by Whittaker (2010b) are virtually identical to those applied by Gillman and Wright (2006), and to those used in the present study. Hillebrand and Cardinale (2010) on the other hand argue that the criteria proposed by Whittaker (2010b) are overly strict, and that accounting for variation among studies in meta-analyses should be recorded and accounted for when interpreting results.

The criteria used for this study replicate Gillman and Wright (2006) in order to maintain consistency, transparency and repeatability of the work. Surprisingly, the difference between the relative frequencies of the different relationships before and after applying the selection criteria was small. This contrasts with the work of Werenkraut and Ruggiero (2011), who reported a change in the relative frequencies of different forms of the altitude–species richness relationship, after applying strict study selection criteria. Here, the main difference after applying strict selection criteria was the reduction in the proportion of non-significant studies.

5.3 Explaining the contrast with Mittelbach et al. (2001)

The predominance of positive A–PSRRs in the literature found in this study contrasts with the commonly held assumption that the "true" (Rosenzweig, 1992) or "ubiquitous" (Huston & DeAngelis, 1994) form of the PSRR is unimodal. The predominance of

positive relationships also contrasts with the finding of Mittelbach et al. (2001) that no form of the A–PSRR was predominant. There are several possible explanations for the difference between the results presented here and those of Mittelbach et al. (2001): (1) the different size of the datasets—the dataset used in these analyses included more cases of the A–PSRR (n = 141) than used by Mittelbach et al. (2001) (n = 88); (2) the greater number of large-scale (i.e. regional and global-to-continental) studies in the dataset in the present study (present study, n = 82, Mittelbach et al. (2001) , n = 51); (3) the fewer number of selection criteria used by Mittelbach et al. (2001) and some inconsistency in their application; and (4) the statistical methods used for classifying the form of the PSRR. Each of these possible explanations is discussed below.

5.3.1 Dataset size

Dataset size is unlikely to be responsible for the difference in conclusions made here with those made by Mittelbach et al (2001) (i.e. predominance of positive and unimodal relationships respectively). The dataset in this study (n = 112 with data re-analysed) had 24 more A–PSRR studies than the one used by Mittelbach et al. (2001) (n = 88 animal species richness relationships). However, there were 52 more positive A–PSRRs reported here than by Mittelbach et al. (2001). They found unimodal relationships were predominant (34.1%) followed by positive relationships (20.5%) (Figure 31). A subset of the dataset from Mittelbach et al. (2001) (n = 37) that was accepted for inclusion in this study was examined to see if 'new' studies (i.e. published after Mittelbach et al.) influenced the overall pattern observed here. Using my methods, both the 'old' (i.e. in the Mittelbach et al. subset) and 'new' subsets produced a predominance of positive relationships (48.6 and 62.5% respectively) and in the 'new' subset, positive relationships were more common than all other relationships combined (proportion test,

$P < 0.0005$) (Figure 32). Furthermore, there was no evidence of a difference between the 'old' and 'new' studies in the relative proportions of the different forms of relationships ($\chi^2 = 7.05$, df = 4, $P = 0.133$). Thus, there is little evidence that the contrast between the results presented here and those reported by Mittelbach et al. (2001) is the result of the larger dataset. The similarities in the proportions of different relationships between the Mittelbach et al. (2001) subset and the 'new' studies do not support this explanation.
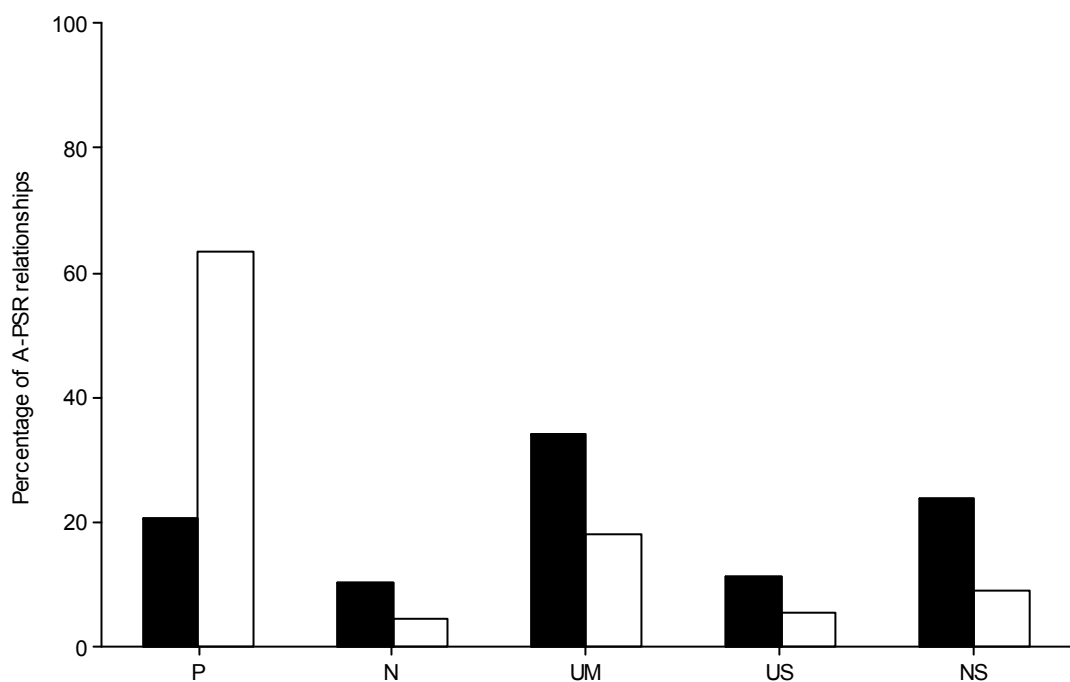
Figure 31. The relative proportions of A–PSR relationships reported by Mittelbach et al. (2001) (black bars, n = 88) and in the present study (n = 112). Relationship codes as in Figure 5.
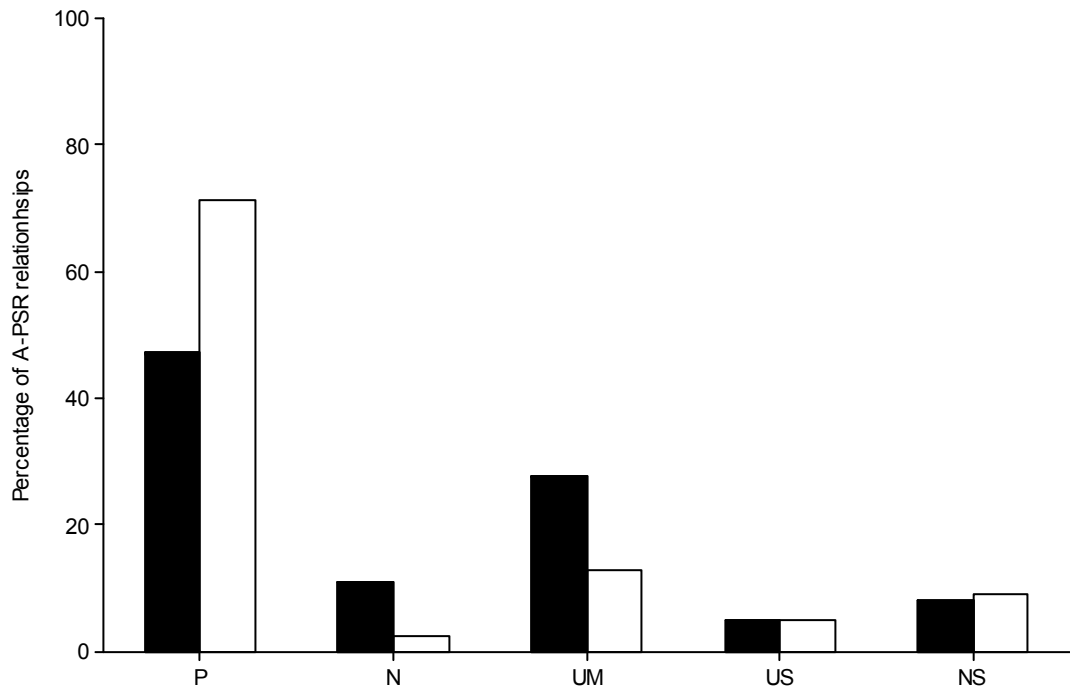
Figure 32. The relative proportions of A–PSR relationships from the Mittelbach et al. (2001) subset included in this study and reclassified using OLS regression, LOWESS line fitting and AICc model selection (black bars), and 'new' studies (Mittelbach et al. subset, n = 36, 'new' subset, n = 76). Relationship codes as in Figure 5.

5.3.2 The influence of macro-scale studies

A second possible explanation might be the presence of a greater number of macroecological studies in the dataset. The dataset compiled by Mittelbach et al. (2001) contained studies up until September 1999; since the mid-nineties the field of macroecology has grown rapidly following the publication of influential volumes on the topic (Brown, 1995; Gaston & Blackburn, 2000; Rosenzweig, 1995), suggesting that the potential for a greater number of macro-scale studies is probable. Whittaker et al. (2001) predicts a positive PSRR across large geographic extents and coarse grains. Therefore, a greater number of macro-scale studies in the dataset used in this study might have affected the overall proportion of positive relationships. However, the proportions of studies at different extents (local-to-landscape, 21.9%; regional, 43.8%; continental-to-global 34.3%) are similar to those used by Mittelbach et al. (2001) (21.5, 40.0, 38.5%

respectively) (Figure 33) ($\chi^2 = 0.335$, df = 2, $P = 0.846$). It should be noted that

Mittelbach et al. (2001) used four geographic extents separating local-to-landscape into

'local' (< 20km) and 'landscape' (20–200km); these two extents were combined for the

above comparison. Moreover, positive relationships dominate at all three extents

examined here, whereas Mittelbach et al. (2001) reported that unimodal relationships

were the most common form of the A–PSRR at the continental-to-global scale,

unimodal and positive relationships were the most common at regional scales, and non-

significant relationships were the most common at the local-to-landscape scale

(combined 'local' and 'landscape'). Therefore, there is no evidence that more macro-

scale studies have contributed a disproportionate number of positive A–PSRRs to the

results presented in this study, firstly because the number of studies at different

geographical extents are proportionately similar in both datasets, and secondly because

positive relationships were predominant at all three geographic extents in this study.
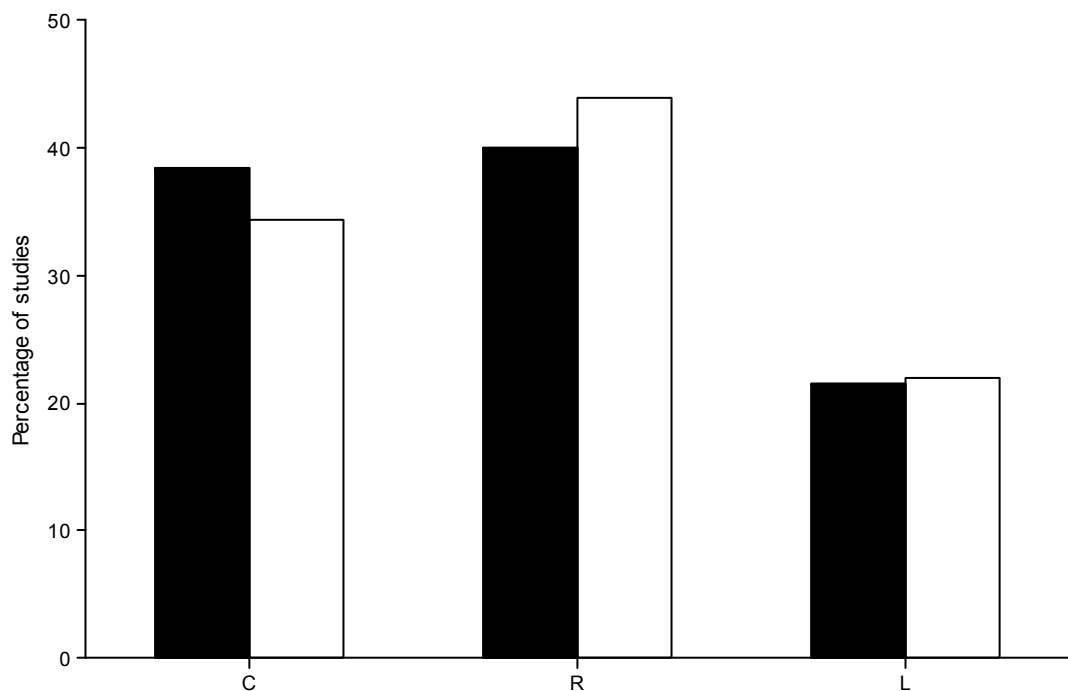
Figure 33. The proportions of studies at different geographical extents in the Mittelbach et al. (2001) data set and the dataset used in this study (M2001 (black bars), n = 65; present study, n = 105). C, continental-global; R, regional; L, local-to-landscape.

5.3.3 The influence of selection criteria

A third factor that might explain the contrast between the results reported by Mittelbach et al. (2001) and those presented here relates to the fewer selection criteria used by Mittelbach et al. (2001). However, despite an *a priori* assumption that selection criteria might influence the final outcome (e.g. Gillman & Wright, 2006; Werenkraut & Ruggiero, 2011; Whittaker, 2010b; Whittaker & Heegaard, 2003), an examination of the data does not support this assumption. Rather, the different methods for classifying relationships were more important in generating the contrasting results.

Mittelbach et al. (2001) had four criteria that a study had to meet to be included in their study; (1) the sample size was ≥ 10; (2) studies were not from "agricultural and intensively managed systems"; (3) studies were not from "systems subject to severe anthropogenic disturbance"; and (4) productivity was not experimentally manipulated. In addition to the criteria used by Mittelbach et al. (2001), six more criteria were used for this study; (1) the sampling regime was held constant; (2) the surrogate for productivity was appropriate for the system being studied, and not liable to distortion from other factors; (3) the study design was not likely to influence the perceived form of A–PSRR; (4) the entire dataset, or part thereof, was not included more than once within the meta-analysis; (5) no other study assessing the A–PSRR was included that covered the same taxon across the same spatial area; and (6) the target taxa were not phylogenetically restricted.

After applying selection criteria (defined above) for the present study, the overall pattern in the entire dataset changed little with positive relationships remaining the most common form of the A–PSRR (see Figures 5 and 6). However, unimodal and non-significant relationships were the most common relationships excluded from the Mittelbach et al. (2001) dataset (33.3 and 29.4% respectively, Figure 34) and positive relationships were the most commonly excluded relationship from the 'new' dataset (i.e.

additional studies identified for the present study) (49.6%, Figure 34). This contrasts

with the findings of Gillman and Wright (2006) who in examining plant–PSRRs

deemed a similar proportion of non-significant (27.3%) relationships, but a higher

proportion of unimodal (52.3%) relationships inadmissible from the Mittelbach et al.

(2001) plant only dataset. The contrast in the relationship forms excluded from the

Mittelbach et al. (2001) component of the dataset and 'new' component of the datasets

makes it difficult to determine if selection criteria influenced the difference between the

results reported in the present study and those reported by Mittelbach et al. (2001).

Therefore, the influence of selection criteria within the Mittelbach et al. (2001) data

subset is examined below.

Unimodal relationships were the most common form of the A–PSRR in the

Mittelbach et al. (2001) data subset before (n = 88) and after (n = 36) applying the

selection criteria used in the present study (Figure 35) and the proportions of different

forms of the A–PSRR were similar (χ^2 =11.758, df = 8, P = 0.161) (Figure 35).

However, after reclassifying relationships for use in the present study (i.e. using OLS

regression, LOWESS line fitting and AIC_c model selection), positive relationships

became the most common form of the A–PSRR in the Mittelbach et al. (2001) data

subset (n = 36) (Figure 35). The predominance of unimodal relationships, as classified

by Mittelbach et al. (2001), before and after applying the selection criteria contrasts

with the predominance of positive A–PSRRs when re-analysed and reclassified for the

present study. This suggests that the methods used for classifying the form of

relationships not selection criteria had a stronger influence on the contrasting results

between the present study and Mittelbach et al. (2001). The influence of relationship

classification is discussed in more detail below (see *5.1.4 The influence of relationship*

classification).
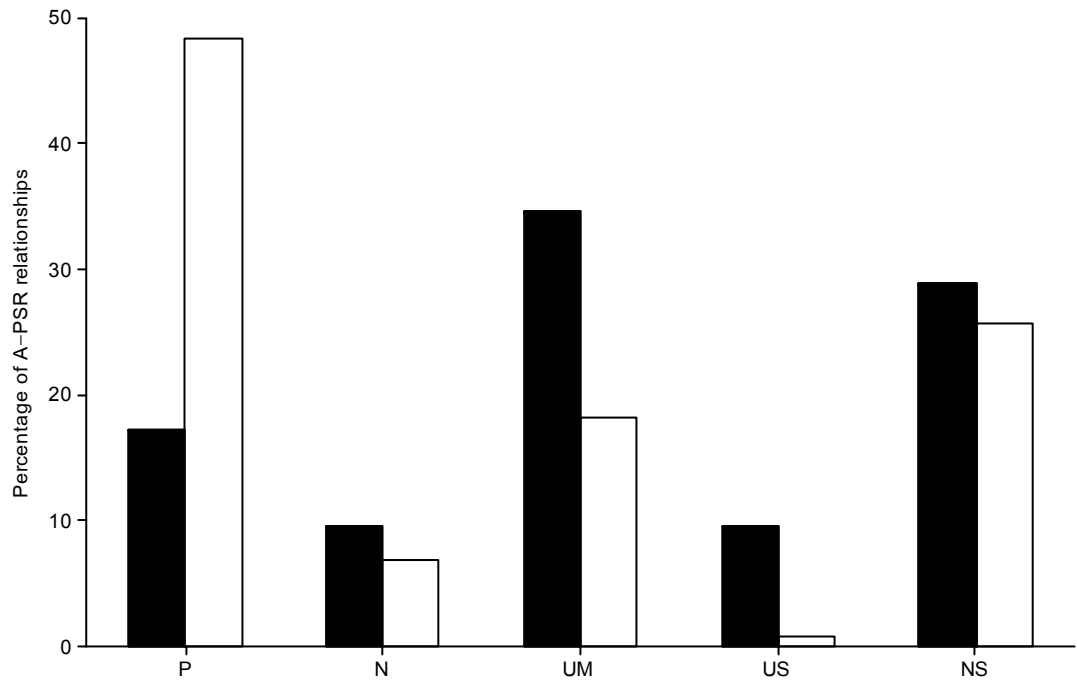
Figure 34. The proportion of different forms of A–PSRRs deemed inadmissible for the present study from the Mittelbach et al. (2001) dataset (as classified by Mittelbach et al. using GLM regression and the MOS-test) (black bars, n= 51), and from the 'new' dataset (n = 132). Relationship codes as is Figure 5.
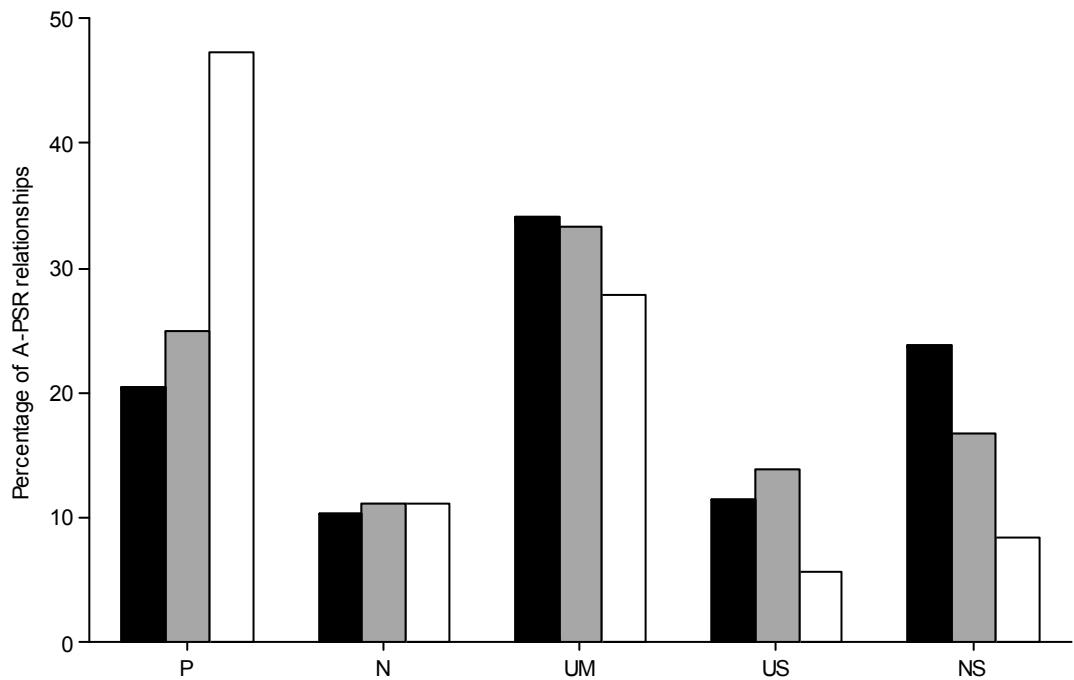
Figure 35. The proportion of different forms of the A–PSRRs from the Mittelbach et al. (2001) dataset before (black bars, n = 88) and after applying selection criteria (grey bars, n = 36) and after reclassifying the relationships using OLS regression, LOWESS line fitting and AIC_c model selection (n = 36). Relationship codes as in Figure 5.

5.3.4 The influence of relationship classification

The methods used for classifying relationships differed between the present study and Mittelbach et al. (2001). Thus, 17 studies that were accepted for inclusion in the present study were classified differently than Mittelbach et al. (2001). An examination of reclassification revealed that 10 studies were reclassified as positive (linear or quadratic), three of which changed from unimodal to decelerating positive (Table 5). Moreover, there were net gains of seven positive relationships and one negative relationship, and a net loss of one u-shaped relationship and equal net losses of three unimodal and non-significant relationships. This suggests that the differences in the results presented here and those reported by Mittelbach et al. (2001) (i.e. positive and unimodal predominance respectively) may be the result of different methods for classifying relationships.

Mittelbach et al. (2001) used a two-step method for classifying relationships: (i) GLM regression (with a Poisson distribution, log-link function and a 10% level of significance); and (ii) the MOS-test for testing for unimodality. The differences in the methods and how they may have contributed to the different results are explored in detail below. Additionally, examples are used to demonstrate how some of the inconsistencies might have been generated.

Table 5. The reclassification of relationships in the present study that were included in Mittelbach et al. (2001). (N = 17)

Reclassification	n	no of accelerating	no of decelerating
Negative to unimodal	1	na	na
Positive to unimodal	1	na	na
Non-significant to unimodal	1	na	na
Non-significant to positive	2	0	1
U-shaped to positive	2	2	0
Unimodal to positive	6	1	3
Non-significant to negative	1	1	0
U-shaped to negative	1	0	1
Positive to u-shaped	1	na	na
Positive to non-significant	1	na	na
Total	17	4	5

(i) Generalised linear model regression

Whittaker and Heegaard (2003) found that the regression methods used by Mittelbach et al. (2001) were likely to have biased their dataset. Mittelbach et al. (2001) used GLM regression with a Poisson distribution and log-link function—in preference to OLS regression—using a 10% level of significance (i.e. $P < 0.1$): while this is generally statistically sound, it might not always be applicable to ecological data. Overdispersion (i.e. the variance exceeding the mean) is common in biological data, and despite methods being available, Mittelbach et al. (2001) did not check, nor correct for, overdispersion where necessary (Gillman & Wright, 2006; Whittaker & Heegaard, 2003). Furthermore, using a 10% level of significance will be biased towards accepting complex relationships that would normally be rejected using 5% level of significance (Whittaker & Heegaard, 2003). By running simulations, Whittaker and Heegaard (2003) demonstrated that the number of unimodal relationships reported by Mittelbach et al. (2001) was likely to be artificially inflated by not checking and/or correcting for overdispersion. Mittelbach et al. (2001) analysed their data using both OLS and GLM regression, but they only reported results for GLM. Among the studies in the Mittelbach et al. (2001) dataset, there was a significant difference in the form of relationships

classified using GLM and the unreported results using OLS regression ($\chi^2 = 11.10$, df = 4, $P = 0.022$) (Figure 36). Unimodal relationships were the most common when GLM regression was used (36.3%) and positive relationships predominated when OLS regression was used (36.4%). Furthermore, the relative proportions of different A–PSRRs classified by Mittelbach et al. (2001) using OLS (n = 88) and, the studies from the Mittelbach et al. (2001) included in the present study (i.e. reclassified using OLS, LOWESS line fitting and AIC_c model selection) (n = 36) were similar ($\chi^2 = 2.85$, df = 4, $P = 0.557$) (Figure 36). Positive relationships were however, more common in the present study (48.6 %) than in the unreported OLS classifications by Mittelbach et al. (2001) (36.4%). The contrast between the GLM and OLS results within the entire Mittelbach et al. (2001), and within the Mittelbach et al. (2001) data subset re-analysed and reclassified for the present study, demonstrates a clear influence of the methods used for classifying relationship forms.
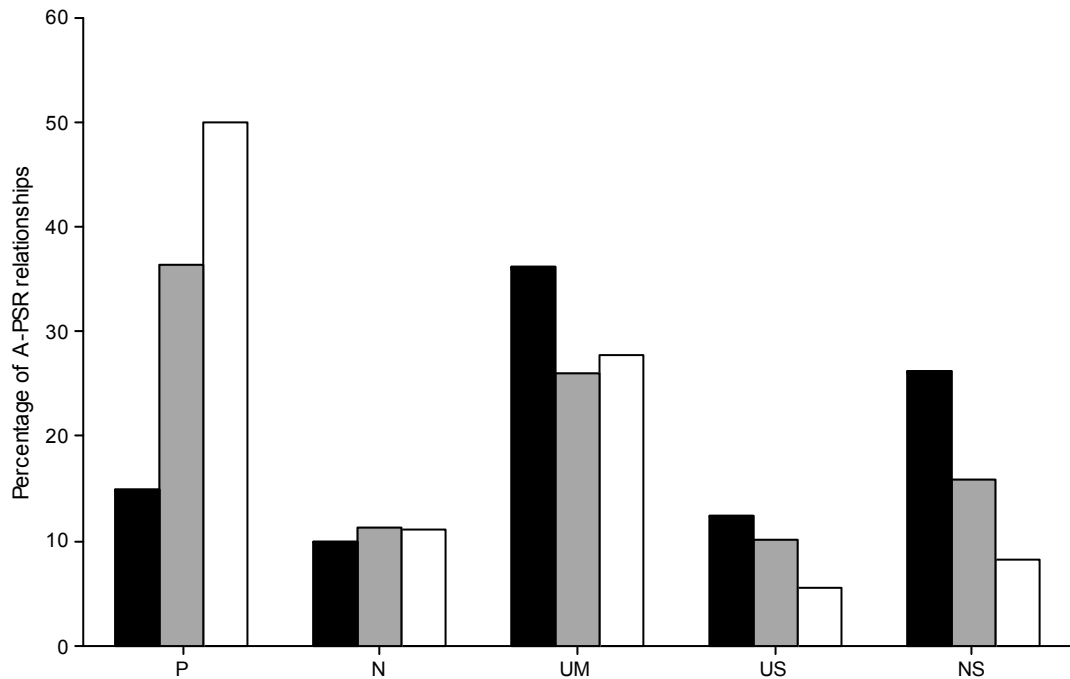
Figure 36. The proportion of different A–PSRRs from Mittelbach et al. (2001) using GLM regression (black bars, n = 80); Mittelbach et al. (2001) using unreported OLS regression (grey bars, n = 88); and the subset of studies from Mittelbach et al. (2001) used in this study using OLS regression, LOWESS line fit and AIC_c model testing (C, n = 36).

(ii) The MOS-test

Unimodal has been suggested to be the 'true' (Rosenzweig, 1992) and 'ubiquitous' (Huston & DeAngelis, 1994) form of the PSRR. Whittaker (2010b) argues that this may have led Mittelbach et al. (2001) and Pärtel et al. (2007) to be "far too generous toward the notion of [a hump]." In other words, when the data showed a significant quadratic term, a hump might have been assumed. However, the presence of a significant quadratic term is not necessarily evidence against monotonicity and caution should be taken in concluding that a relationship is unimodal (Murtaugh, 2003). In ecology and evolution, researchers are often interested in whether the relationship between particular response and predictor variables is monotonic or, unimodal or u-shaped (e.g. the PSRR). Thus an objective method for testing for an internal minimum or maximum is desirable.

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Starting with Leibold (1999), a number of researchers interested in the form of the

PSRR (e.g. Chase & Leibold, 2002; Chase & Ryberg, 2004; Ding, Yuan, Geng, Lin, &

Lee, 2005; Dodson et al., 2000; Hoffmann & Dodson, 2005) have used a test developed

by Mitchell-Olds and Shaw (1987; the MOS-test) for detecting unimodal relationships

in models of natural selection: this is the same test employed by Mittelbach et al.

(2001). Two issues can be identified that need to be addressed when using this

approach. The first issue is one initially addressed by Mitchell-Olds and Shaw (1987, p.

1155) and relates to fundamental statistical practice:

> it is imperative to look carefully at the data. Graphical analysis is an
> essential step in regression analysis....in order to determine whether
> the data fit the hypothesized model and to detect possible unexpected
> patterns or problems in the data

That means indiscriminately applying the MOS-test—or any other statistical test— to

data and interpreting a significant p-value as evidence of a unimodal or u-shape is

inappropriate. Data should always be examined visually before statistical testing.

The second issue with the MOS-test is addressed by Murtaugh (2003) and relates

to the high rate of rejection of monotonicity when using 'quadratic tests' (e.g. MOS-

test). Using such tests, a unimodal or u-shape is inferred when a maximum or minimum

falls within the observed range of values (i.e. MOS-test). However, 'this is almost

always the case' in quadratic relationships, even those with non-significant quadratic

terms (Murtaugh, 2003). Murtaugh found that over 99 percent of tests failed to reject a

null hypothesis of unimodality despite data being drawn from distributions that were not

unimodal. Therefore, there is a high probability of classifying any quadratic relationship

(i.e. decelerating, accelerating, asymptotic or, unimodal) as unimodal, indicating a bias

toward unimodal relationships. Indeed, after Mittelbach et al. (2001) applied the MOS-

test, all relationships with 'significant' (P < 0.10) quadratic components according to GLM regression (39 studies) were classified as unimodal or u-shaped.

The methods used in the present study (i.e. OLS regression, LOWESS curve fitting and AIC_c model selection) may have been too liberal toward detecting decelerating positive relationships. However, it is important to note that some of the relationships classified as unimodal by Mittelbach et al. (2001) did not have statistically significantly quadratic terms and were subsequently classified as decelerating positive in the present study. The evidence presented above and the demonstration by Whittaker and Heegaard (2003) suggest that the methods employed by Mittelbach et al. (2001) were biased towards unimodal relationships. Therefore, it is unsurprising that there were a lower proportion of unimodal relationships presented here in contrast to the predominance of unimodal relationships reported by Mittelbach et al. (2001). The methods used in the present study do not have a systematic bias towards any particular relationships form. Plotting the data and visually examining a LOWESS fit gives an estimation of the trend in the data allowing the detection of a down- or upward trend. This is important given the contention that has arisen regarding positive or unimodal PSRRs (Gillman & Wright, 2006; Mittelbach et al., 2001; Whittaker & Heegaard, 2003). Furthermore, the assumptions of OLS regression (i.e. normality and symmetry of errors) are less likely to be violated than the assumption of Poisson errors in GLM regression in species richness data (Gillman & Wright, 2006). Therefore, OLS regression was more appropriate for use in the present study. The additional step of using AIC_c model selection provided important information for differentiating monotonic relationships from decelerating and accelerating relationships, a factor not considered by previous meta-analyses. This step was important to distinguish how previous studies might have misclassified decelerating positive relationships as unimodal.

5.3.5 Examples of inappropriate relationship classification

Four examples of the issues related to the methods used by Mittelbach et al. (2001) are presented below: (i) an example related to the problem with applying statistical analyses without visually examining the data first; (ii) a misclassification of a decelerating positive relationship as unimodal in the absence of evidence of a downturn; (iii) a misclassification of a decelerating negative as u-shaped with evidence refuting an upturn at high productivities; and (iv) a relationship classified as unimodal by GLM, with a 10% level of significance that shows no evidence of any relationship at all.

(i) Visual examination

Before applying any statistical technique to data it should always be visually examined to identify general patterns and any unusual observations. For regression, the data should be reasonably scattered across the whole length of the inferred regression (Fowler, Cohen, & Jarvis, 2008). Palomäki and Paasivirta (1993) was included by Mittelbach et al. (2001) using phosphorous as a surrogate for productivity. Eleven sites were sampled with phosphorous levels ranging from 5–55µg/l with 10 of the 11 sites ranging from, 5 to15µg/l. The site with highest phosphorous concentration, however, was three and a half times higher than the next highest measure of phosphorous and thus represents an outlier that deviates from the general trend of the data. This last data point would have had an overwhelming influence on the quadratic fit (Figure 37). The discontinuity in the data invalidates the use of regression because any departure from an apparent trend cannot be inferred with the absence of internal data. In this case, the number of different taxa increased between 5 and 15 µg/l P, but the highest phosphorus level corresponded with the lowest diversity in the dataset. Based on these data, Mittelbach et al. (2001) inferred a hump-shaped relationship using GLM regression.

However, extreme outliers result in overdispersion in Poisson GLM regression (Zuur, Ieno, & Elphick, 2010) (see *5.1.4 The influence of relationship classification* for a discussion on GLM and overdispersion above). This conclusion by Mittelbach et al. (2001) is in contrast to the conclusions drawn by Palomaki and Paasivirta (1993) who reported that phosphorous could not explain the variation in the number of taxa in their study. Interestingly, biomass data were also reported by Palomäki and Paasivirta (1993) and biomass had a positive relationship with the number of different taxa (Figure 38) and the highest phosphorous value corresponds with the lowest biomass value. Therefore, not only is the use of regression on the phosphorous–number of different taxa data invalid, but it appears that phosphorous is a poor proxy for productivity in the study system. Mittelbach et al. (2001) provide no explanation why the phosphorous was chosen instead of biomass when biomass was commonly chosen in other cases.
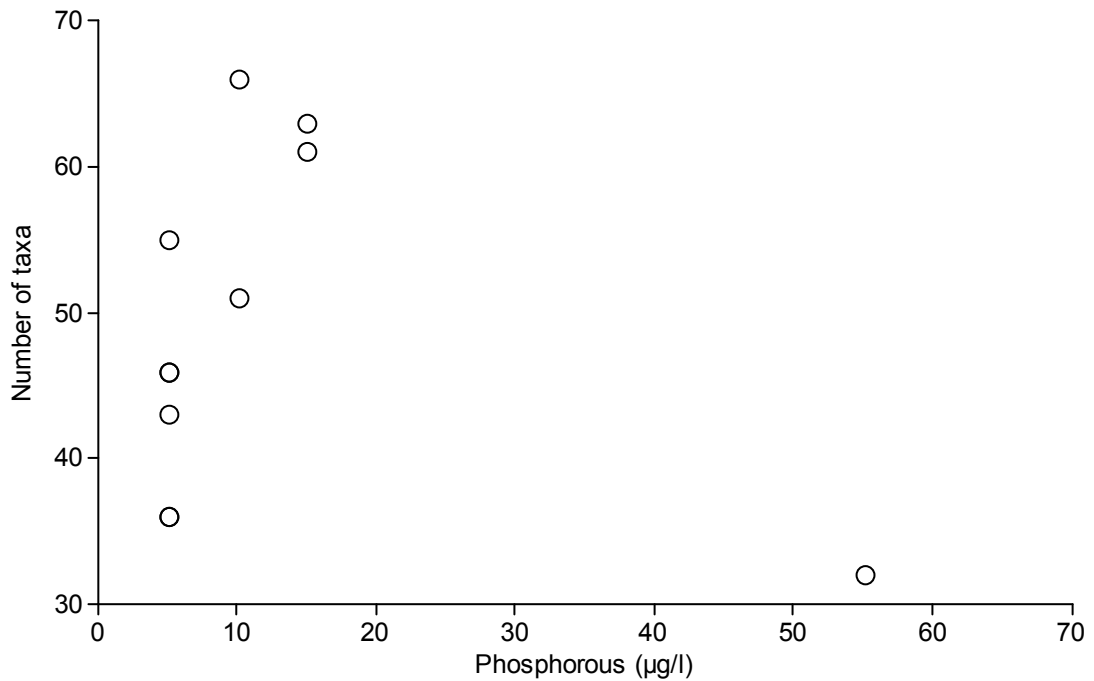
Figure 37. An example of data classified as unimodal by Mittelbach et al. (2001) using GLIM regression and the MOS-test. The large gap in the data between 15 and 55 µg/l P invalidates the use of regression and interpolating a hump is highly questionable. Data obtained from the data table published in Palomäki and Paasavirta (1993) (N = 11).
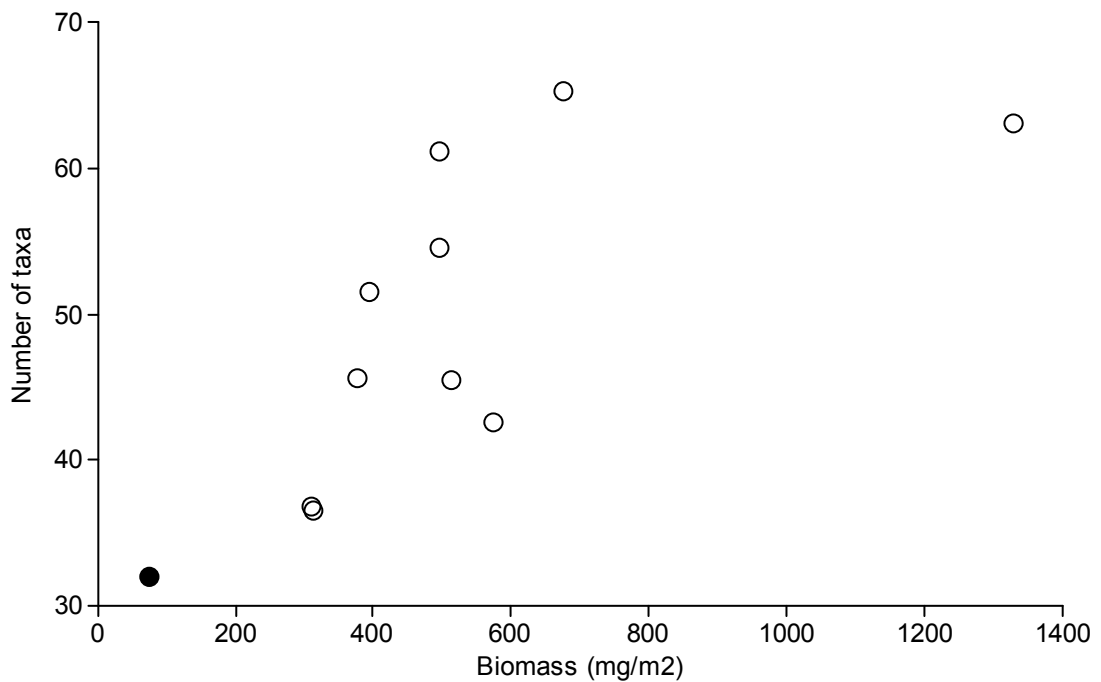
Figure 38. The relationship between species richness and biomass presented by Palomäki and Paasavirta (1993). The positive relationship contrasts with the 'unimodal' relationship reported by Mittelbach et al. (2001) using phosphorous as a surrogate (Figure 33) (N = 11). The solid point corresponds to the highest P value in Figure 37.

(ii) Unimodal misclassification

Death and Winterbourne (1995) measured epithelic phytopigment concentration (μg/cm^2) in streams as a surrogate for productivity and related it to macroinvertebrate species richness. The relationship was presented as positive (R^2 = 53%) by the primary authors, who stated that "[a] quadratic model for the relationship only improved the fit by 9 percent." Mittelbach et al. (2001) however, classified the relationship as unimodal. A re-analysis done for the present study agrees with the findings of the Death and Winterbourne (1995). By plotting the data with a LOWESS line, there is no evidence of a downward trend at the high end of the productivity scale (Figure 39A). After applying AIC$_c$ it was determined that the quadratic model fit the data best, indicating a decelerating positive relationship (quadratic R^2 = 54.4%, P < 0.0005, linear AIC$_c$ = 399.44, curvilinear AIC$_c$ = 388.90). Fitting a quadratic curve with 95 percent confidence intervals demonstrates the increasing uncertainty of the downward curve at high levels of phytopigment concentration (Figure 39B). Moreover, the upper-bound of the 95 percent confidence interval shows no evidence of a down turn.
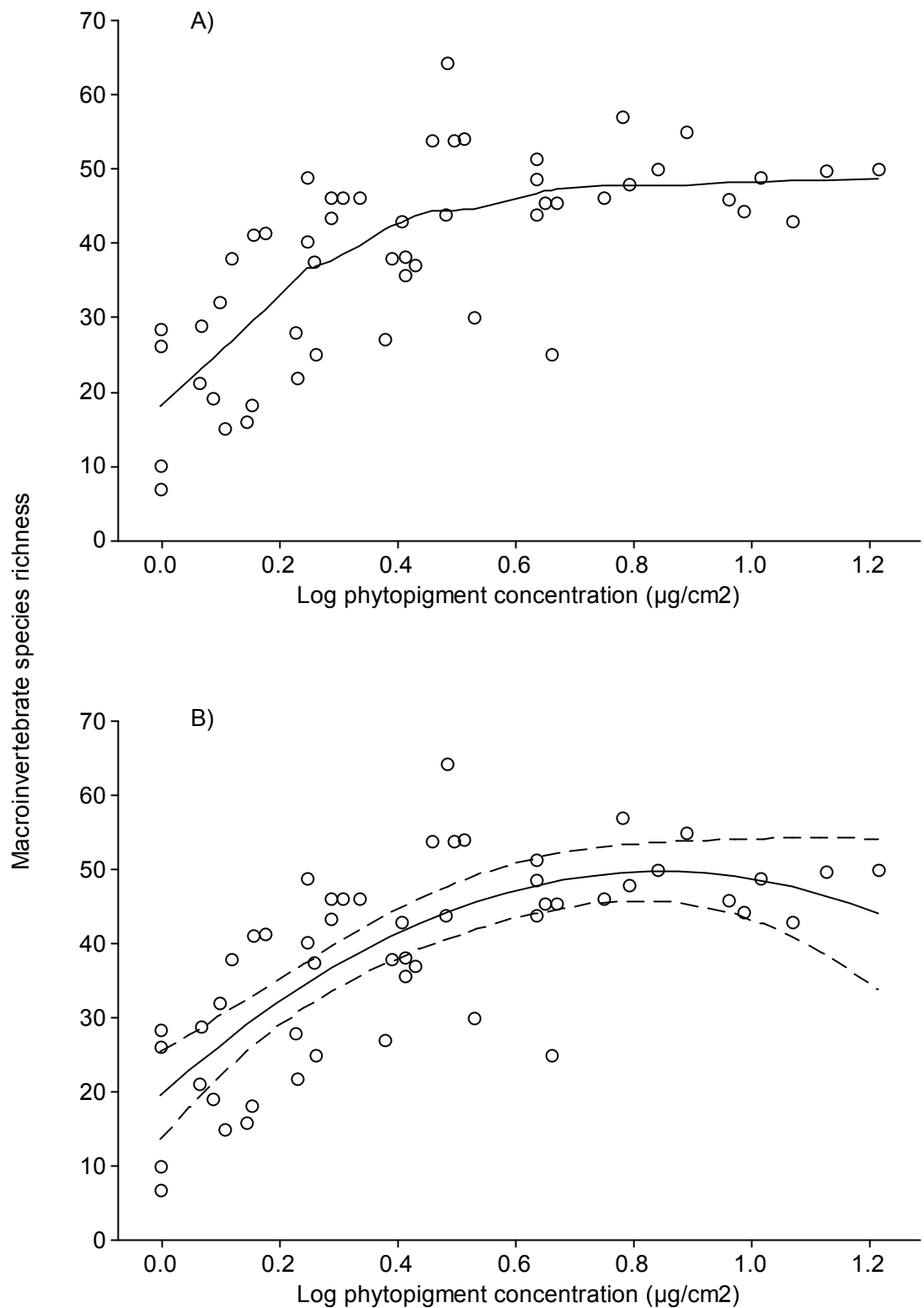
Figure 39. (A) A demonstration of a relationship classified by Mittelbach et al. (2001) that was reclassified as decelerating positive in the present study given the lack of evidence of downturn of a fitted LOWESS line. (B) A quadratic fitted (with 95 % confidence interval) to the same data as (A) to demonstrate the increasing uncertainty of the downward curve of the relationship (B). The data were digitised from the figure presented in Death and Winterbourne (1995) (N = 53).

(iii) U-shaped misclassification

Owen (1988) measured rodent species richness and related it to primary productivity ($g/m^2/yr$) finding a negative relationship. Mittelbach et al. (2001) re-analysed the data and classified the relationship as u-shaped. After plotting the data that were digitised from Owen (1988) and fitting a LOWESS curve there was evidence of levelling off and no upward trend in species richness at the upper end of measured productivities (Figure 40A). Moreover, fitting a third order polynomial (with a 95% confidence interval) suggests a decline in richness at high productivity (Figure 40B) providing strong evidence against a u-shape in these data. This is consistent with the results presented by Owen (1988). Thus, in the present study, a decelerating negative was concluded after using OLS regression, fitting a LOWESS line and AIC_c model selection (quadratic $R^2 = 56.4\%$, $P < 0.0005$, linear $AIC_c = 886.76$, curvilinear $AIC_c = 851.77$).
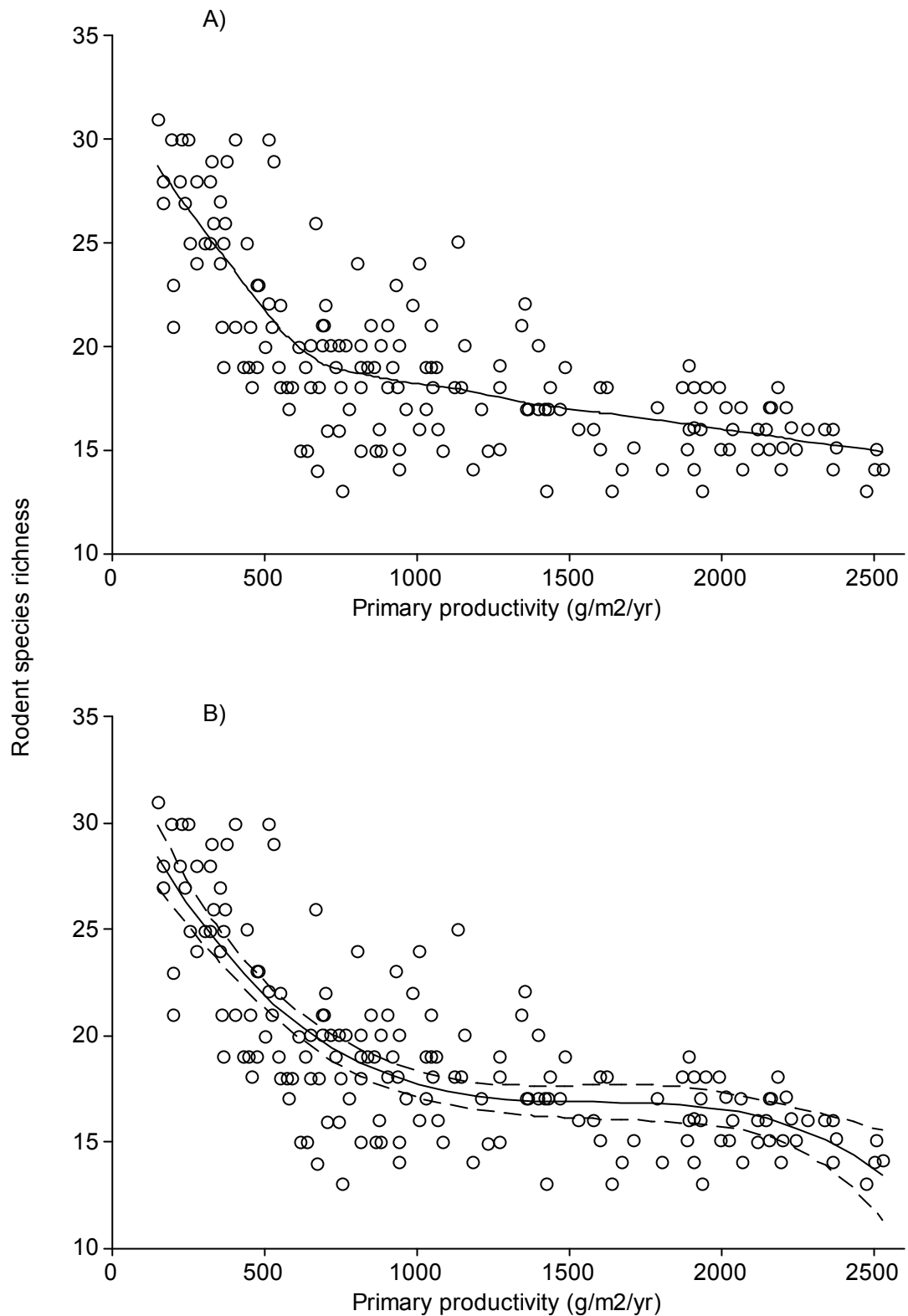
Figure 40. (A) A demonstration of a relationship classified by Mittelbach et al. (2001) as u-shaped that a fitted LOWESS line shows no evidence of an upturn in the data at high levels of productivity. (B) A third order polynomial fitted (with 95% confidence intervals) to the same data as (A) suggesting a downturn in species richness at high levels of productivity refuting the claimed u-shape by Mittelbach et al. (2001). The data were digitised from the figure presented by Owen (1988) (N = 171).

(iv) Liberal classification of unimodal relationships

The following example was presented by Gillman and Wright (2006) to demonstrate how liberal GLIM regression with a 10% level of significance is at classifying spurious relationships as unimodal. Gough et al. (1994) presented a relationship between biomass and plant species richness classifying the relationship as non-significant. Mittelbach et al. (2001) presented a GLIM unimodal result with a 'significant' quadratic component ($P = 0.016$). OLS on the other hand was non-significant using a 5% level of significant ($R^2 = 12.9\%$, quadratic model, $P = 0.110$; quadratic term, $P = 0.095$). A visual examination of the data shows no obvious relationship (Figure 41).
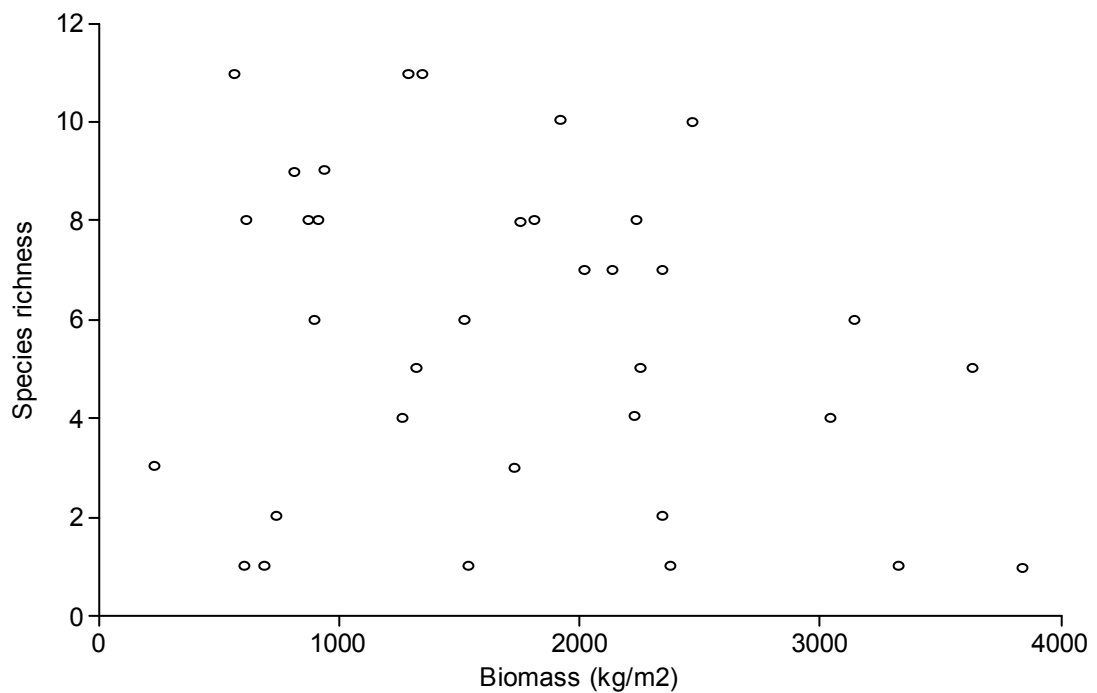
Figure 41. A relationship classified by Mittelbach et al. (2001) as unimodal using GLIM regression and the MOS-test (P = 0.016) despite the lack of relationship indicated by the scatterplot and OLS regression ($R^2 = 12.9\%$, quadratic model, $P = 0.110$; term, $P = 0.095$). Data digitised from Gough et al. (1994) (N = 35).

5.4 Conclusions on explanations for contrasting results

Dataset size did not influence the contrast between the results of the present study and Mittelbach et al. (2001). Both the subset of Mittelbach et al. (2001) studies (as classified for the present study), and the subset of more recent studies included in the present study showed a predominance of positive relationships, providing evidence that positive relationships were the most common form of the A–PSRR in both datasets. The additional macro-scale studies present in the more recent studies published after Mittelbach et al. (2001) did not contribute a disproportionate number of positive A–PSRRs the present study. Despite the presence of more large scale studies in the present study, the relative proportions of studies at different scales was similar in both datasets. Furthermore, positive relationships were predominant at all three geographical extents in the present study. Selection criteria did not appear to greatly influence the differences between the results of Mittelbach et al. (2001) and the results in the present study. Across the whole dataset, positive relationships were the most common form of the A–PSRR before and after selecting only studies that were robust tests of the A–PSRR. The different methods used for analysing relationships is the most plausible explanation for the contrasting results presented in this study and the results reported by Mittelbach et al. (2001). Furthermore, the examples of misclassification, inappropriate statistical application and questionable classification using GLM, and the demonstration by Whittaker and Heegaard (2003) that GLM regression may have inflated the number of unimodal relationships in the Mittelbach et al. (2001) dataset, suggest a systematic bias towards unimodal relationships using the methods employed by Mittelbach et al. (2001). Therefore, given this bias towards hump-shaped relationships in previous studies, it can be concluded that positive relationships are the most common form of the A–PSRR. This conclusion is consistent with the results presented by Gillman and Wright (2006) who found positive relationships were predominant for terrestrial plants.

5.5 The influence of scale

5.5.1 Geographic extent

The form of the PSR relationship is hypothesised to vary with scale in both plants (Scheiner & Jones, 2002) and animals (Chase & Leibold, 2002). At smaller scales the form of the relationship is proposed to be hump-shaped or more variable, but at larger scales the relationship is proposed to be monotonic and positive (Chase & Leibold, 2002; Mittelbach et al., 2001; Waide et al., 1999; Whittaker et al., 2001). Furthermore, some have proposed (e.g. VanderMeulen, Hudson, & Scheiner, 2001; Whittaker et al., 2001) that the observed positive PSRR at broad geographic extents is the result of hump-shaped relationships at smaller scales with successively higher beta-diversity with increasing productivity. The predominance of positive relationships at all scales in the present study contrast with these predictions and the results of Mittelbach et al. (2001). Indeed, positive relationships were overwhelmingly predominant at the continental-to-global extent and, despite the form of the relationship being more variable and unimodal increasing in frequency at the two smaller extents, positive relationships were also predominant at smaller scales. Moreover, positive relationships had the highest mean effect size at the continental-to-global and local-to-landscape scales. Although negative relationships had the highest mean effect size at the regional scale, positive relationships were overall more important given the low frequency of negative relationships at all scales (4.5% in the entire dataset). Similarly, at the regional scale u-shaped relationships can be considered unimportant.

The predominance of positive relationships might result from classifying curvilinear relationships for which no evidence of a turning point exists as decelerating and accelerating rather than as unimodal or u-shaped relationships as has been done in the past. This is of particular interest with regard to unimodal and decelerating positive

relationships given the prediction of unimodal predominance at small scales and positive relationships at progressively larger scales. Collapsing decelerating positive relationships into unimodal relationships produces an increasing frequency of unimodal relationships with decreasing geographic extent (Figure 42). This suggests that the previously perceived influence of scale on the form of the relationship may to some extent be an artefact of Mittelbach et al. (2001) being too liberal toward unimodal relationships at smaller scales. Therefore, decelerating positive relationships become more common with decreasing geographical extent.

Another explanation for the predominance of positive and decelerating positive relationships at small extents relates to the range of productivity measured. At small extents, the ranges in productivity will tend to be small, and studies at small extents might fail to capture the entire range of productivity for the given habitat. Therefore, a decelerating relationship might represent the beginning of a downturn of a unimodal relationship. Nonetheless, in the absence of evidence of a downturn, a hump-shape cannot be inferred, because this amounts to an assumption about theory which in turn is used to provide evidence in favour of the theory.
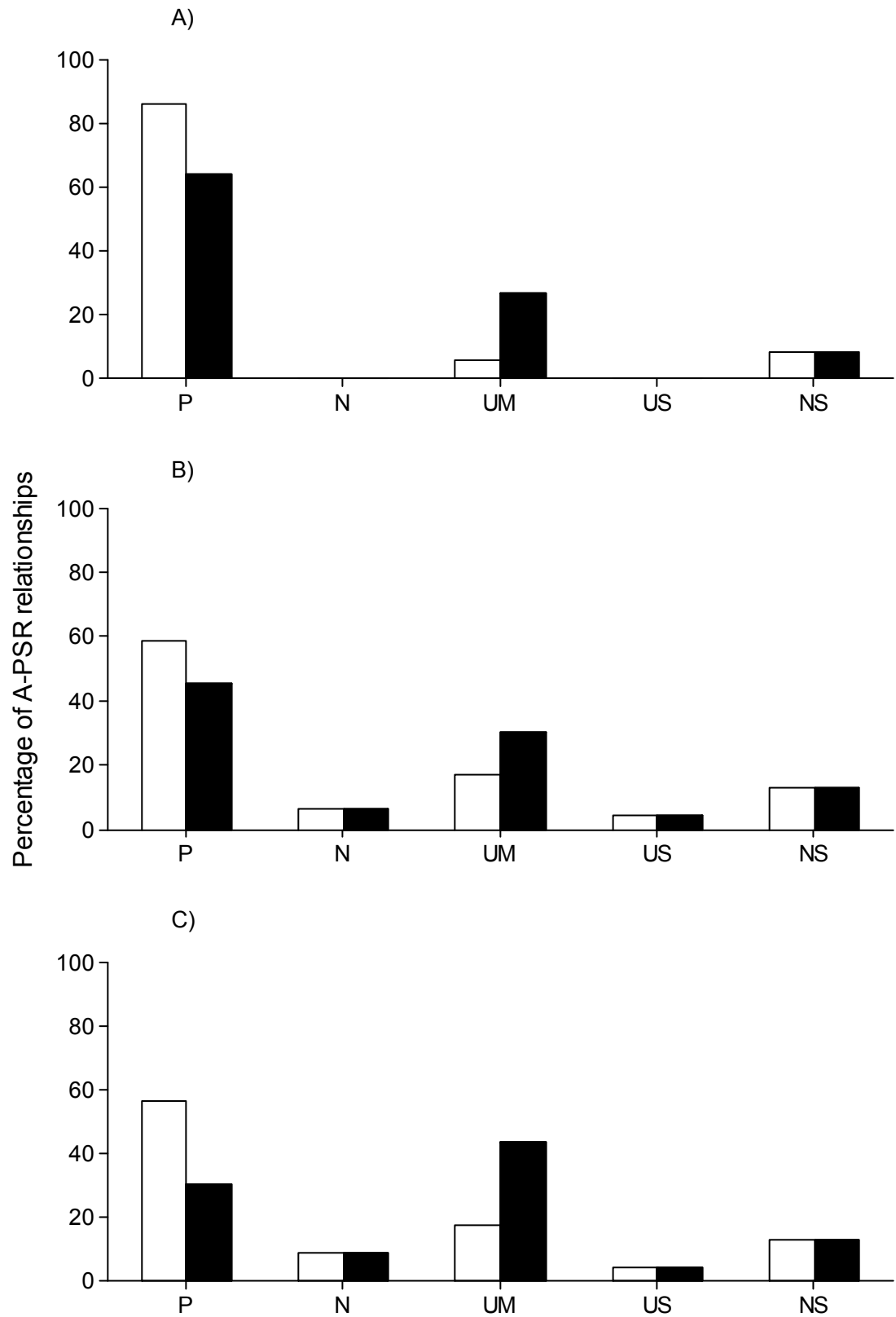
Figure 42. The proportion of different A-PSR relationships at different geographical extents, before and after (black bars) hypothetically collapsing decelerating positives into unimodal relationships. (A) Continental-to-global (n = 36); (B) regional (n = 46); (C) local-to-landscape (n = 23). Relationship codes as in Figure 5.

At the regional scale one of the two negative relationships (Owen & Dixon, 1989) represented the relationship between lizard richness and a multivariate measure of 'wetness' in an arid region. In the same study, a positive relationship was found for frogs and toads, turtles and salamanders. This could be related to physiological and biological differences between lizards and the other groups. Owen and Dixon (1989) infer that because lizards are physiologically independent of water for reproduction and heliothermic (i.e. require sunlight for thermoregulation), the wetter areas might suppress lizard activity. This contrarian relationship between lizards and other vertebrate groups (i.e. mammals, birds and amphibians) has also been demonstrated in Australia with lizard richness peaking in the dry desert (Powney, Grenyer, Orme, Owens, & Meiri, 2010). Along with differential responses to environmental variables, Powney et al. (2010) conclude that centres of diversification differ between lizards and other groups, accounting for this non-congruence. Hence, while negative relationships may be observed in taxonomically restricted groups due to their physiological requirements, a broader investigation (e.g. total vertebrate richness) is likely to have a different form of the PSRR. One of the two negative relationships at the local-to-landscape scale related ant richness to NPP (Sanders, Lessard, Fitzpatrick, & Dunn, 2007). However, the levels of NPP were relatively high and the range was narrow, indicating the negative relationship could reflect the downward curve of a unimodal relationship (Rosenzweig, 1992). However, Sanders et al. (2007) found that ant richness was strongly and positively related to temperature, and suggest that across the scale of study temperature is more important than NPP in regulating ant activity.

5.5.2 Grain

Whittaker and Heegaard (2003) argue that grain is a the most important component of scale in determining patterns of diversity. Furthermore, combining coarse- and fine-grain studies is inappropriate since different components of diversity are sampled at different grains. Fine-grain samples alpha-diversity, and coarse grain-samples beta-diversity. Alpha-diversity is more strongly influenced by migration, whereas beta-diversity is more strongly influenced by longer term process like speciation (Whittaker et al., 2001). After separating the studies into fine and coarse grain, there was indeed a difference with unimodal relationships being more common in fine grained studies. Nonetheless, positive relationships were predominant at both grains which is similar to the patterns found for terrestrial plants (Gillman & Wright, 2006). These results contradict the prediction that hump-shaped relationships dominate at fine grains although they are more common than at coarse grains (Chase & Leibold, 2002). Furthermore, other studies have found that the form of the PSRR does not vary with grain (Kaspari et al., 2000) suggesting that the form of the PSRR is not universally grain dependent.

There were more than twice as many coarse- (n = 69) than fine-grain (n = 29) studies in the dataset, many of which constitute spatial analyses using geographic information systems (GIS) grid squares. The size of grid squares can vary from study to study, with some using 220 × 220 km (approx 48,400km^2) (Hawkins & Porter, 2003b) and others using smaller 20,000km^2 grid cells (Hurlbert & Haskell, 2003). However, across such large scales, despite the doubling in grid cell size, the same component of diversity is being sampled (i.e. beta diversity). van Rensburg et al. (2002) demonstrated no qualitative difference in the relationships between birds and AET in southern Africa

when using half, one and two degree grid cells. Therefore analysing coarse-grain studies of these scales together is appropriate.

Chase and Leibold (2002) found that the PSRR was different using the same dataset when they aggregated it at different grains (ponds and watersheds); the PSRR was humped at the 'pond' grain and positive at the 'watershed' grain. If decelerating positive relationships were collapsed into unimodal relationships (a probable result if using GLM regression and the MOS-test), positive relationships would remain predominant at the coarse grain (73.9 to 53.2%) (Figure 43A). Whereas, positive and unimodal A–PSRRs would become equally common (37.9%) among fine-grain studies (Figure 43B). While doing this might make the results more consistent with studies such as Chase and Leibold (2002), in which it is claimed that the type of relationship is entirely scale dependent, the large number of positive relationships at fine grains is still contradictory to this assertion. Importantly, as discussed with regard to geographical extents, there is little evidence to suggest that decelerating positive relationships should be classified as unimodal.
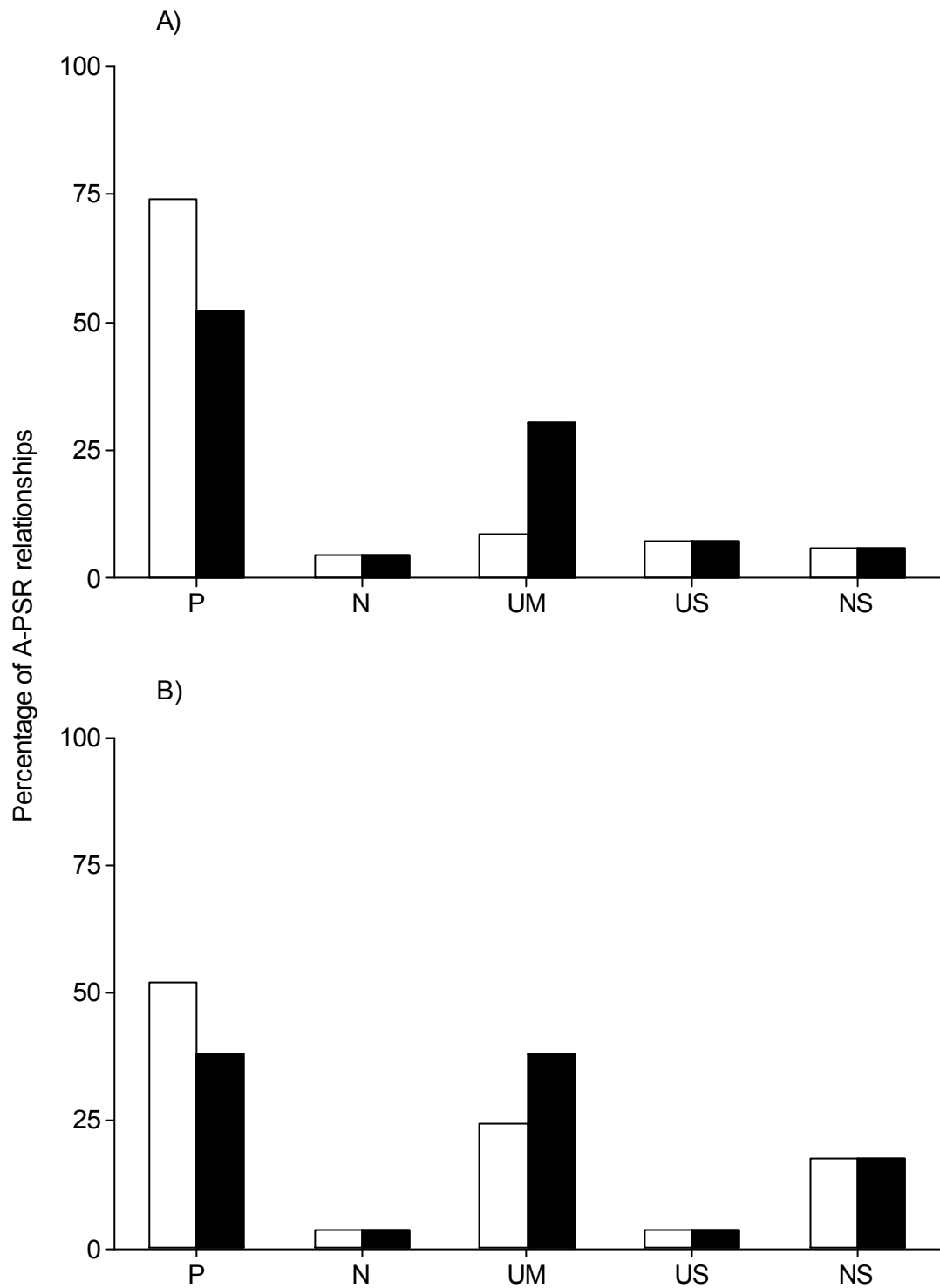
Figure 43. The proportion of different A-PSR relationships at coarse (A, n = 69) and fine (B, n = 29) grains before and after (black bars) hypothetically collapsing decelerating positives into unimodal relationships. Relationship codes as in Figure 5.

5.6 The influence of ecosystem type

Terrestrial species richness patterns have received more attention than aquatic systems, particularly at large scales (Heino, in press). Here there were more than twice as many terrestrial A–PSRR studies than studies in marine and freshwater systems combined. Similar proportions of freshwater and terrestrial studies were examined by Mittelbach et al. (2001). Moreover, the relative proportion of studies in terrestrial and aquatic ecosystems was similar to previous reviews of the A–PSRR (Mittelbach et al., 2001; Waide et al., 1999). However, the results are in contrast. Both Mittelbach et al. (2001) and Waide et al. (1999) reported unimodal relationships as predominant in aquatic environments whereas positive relationships were the most common form of the A–PSRR in the present study. It should be noted that both of the previous studies did not examine freshwater and marine habitats separately. Waide et al (1999) found positive relationships predominated in terrestrial systems consistent with the results presented here. Mittelbach et al. (2001), however, reported hump-shaped A–PSRRs as the most common relationship in terrestrial habitats.

5.6.1 Terrestrial

Plant species richness is positively related to productivity at regional and continental-to-global extents (Gillman & Wright, 2006) and global terrestrial richness of vertebrate consumers is positively related to producer richness (Jetz, Kreft, Ceballos, & Mutke, 2009). Thus, at least at larger scales, the predominance of positive A–PSR relationships and congruence with plant species richness is unsurprising, despite the contrast with the findings of Mittelbach et al. (2001). The idea that diversity begets diversity has been around for at least 50 years (Hutchinson, 1959), but the underlying causal mechanisms are uncertain. Species richness of taxa might correlate with the richness of other taxa for

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a number of reasons: (1) consumer richness may be linked to producer richness through trophic cascading and resource diversity (Hutchinson, 1959); (2) producer and consumer richness may be controlled by the same external factors such as energy or productivity (Hawkins & Porter, 2003a; Wright, 1983); or (3) taxa might respond similarly to different collinear factors (e.g. temperature and productivity). A number of studies have found a positive correlation between plant and animal richness (e.g. Currie, 1991; Hawkins & Porter, 2003a; Siemann, Tilman, Haarstad, & Ritchie, 1998). However, a recent meta-analysis of inter-taxa diversity relationships found only ~35% of the studies examined reported significant correlations with a relatively low mean *r*-value (0.374) (Wolters, Bengtsson, & Zaitsev, 2006). Furthermore, both Currie (1991) and Hawkins and Porter (2003a) found stronger relationships between vertebrate richness (excluding amphibians) and PET and, butterfly richness and AET respectively than with plant species richness. This suggests that consumer species richness is likely to be more strongly influenced by the same or collinear factor that influences plant species richness rather than dependence between the two. The evidence presented in the present study and by Gillman and Wright (2006) suggests that productivity is an important factor in determining species richness of both plants and animals, and that the relationship between the two is predominantly positive.

5.6.2 Freshwater

Positive A–PSRRs predominated in freshwater ecosystems. This contrasts with previous studies that found that unimodal relationships were the most common form of the PSRR in aquatic ecosystems (e.g. Dodson et al., 2000; Mittelbach et al., 2001; Waide et al., 1999). In the case of Mittelbach et al. (2001) the predominance of unimodal relationships is most likely due to their methods having a bias towards unimodal

relationships (see *5.1.4 The influence of relationship classification*). However, unimodal relationships were more common in freshwater systems than in terrestrial studies. There are three possible explanations why there was a greater proportion of unimodal relationships found in freshwater systems than terrestrial studies: (i) the surrogates for productivity in freshwater systems may not have a linear relationship with productivity; (ii) as mentioned above, studies are more commonly undertaken in freshwater ecosystems across smaller scales; and (iii) all but one (Hoyer & Canfield, 1994) of the studies in freshwater systems consisted of poikilothermic taxa (see *5.5.2 Poikilotherms* for discussion on poikilotherms).

(i) Surrogates

Of the productivity surrogates used in freshwater systems, nutrient concentrations are the most problematic. Higher levels of phosphorous and nitrogen might allow high productivity, but productivity can be confounded by toxicity because high nutrient concentrations result in eutrophic conditions (Camargo & Alonso, 2006). However, there was only one relationship included in the present study in which nutrient concentration (phosphorous in this case) was used as a productivity surrogate and it was classified as a positive A–PSRR. Moreover, the surrogates used in freshwater studies were commonly direct measures of productivity (e.g. algal biomass accrual and ^{14}C fixation rate). Therefore, unimodal relationships in this dataset cannot be attributed to surrogate selection.

(ii) The influence of scale

Studies of freshwater systems have historically covered small spatial scales with less focus on macro-scales (Heino, in press). The PSRR is hypothesised to be more variable

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and/or unimodal at smaller scales (Chase & Leibold, 2002; Whittaker et al., 2001). Therefore, the greater variability in the form of the A–PSRR, and higher frequency of hump-shaped relationships in freshwater ecosystems presented here could be attributed to a lower proportion of macro-scale studies. Indeed, studies at the local-to-landscape extent (39.1%) were more common than at the continental-to-global extent (26.1%) within freshwater studies in the present meta-analysis. Nonetheless, considering regional and continental-to-global both as macro-scale, there are almost twice as many large-scale studies in the dataset used in the present study. Therefore, large-scale studies may have contributed a disproportionate number of positive relationships to the freshwater dataset. Indeed, positive relationships predominated the continental-to-global extent (85.7%), were the most common form of the A-PSRR at the regional extent (62.3%), and local-to-landscape extent (44.4%) (Figure 44). However, given that unimodal relationships were more common at the smallest extent, and there were more studies at the smallest extent, these studies may have contributed to the higher proportion of unimodal relationships in freshwater systems than terrestrial studies. The predominance of positive relationships at macro-scales on the other hand, does not account for the observed pattern of positive predominance across all freshwater studies because positive relationships were the most common form of the A–PSRR at all scales.
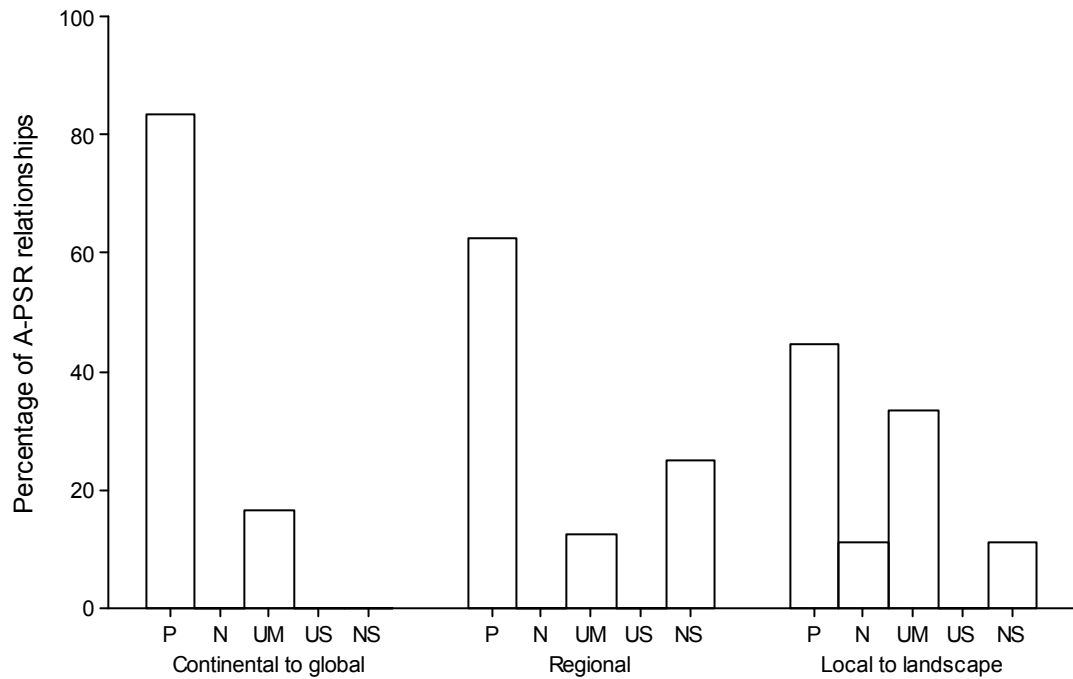
Figure 44. The proportion of different A–PSR relationships in freshwater systems, at three geographical extents. Continental-to-global, N = 6; regional, N = 8; local-to-landscape, N = 9. Relationship codes as in Figure 5.

5.6.3 Marine

The relative frequencies of A–PSRRs in marine ecosystems were in contrast to all other categories presented here. The marginal predominance and accompanying strength of hump-shaped relationships is more consistent with Mittelbach et al. (2001) than any other grouping used in the present meta-analysis. There are four potential explanations for the unimodal relationships observed in marine systems: (i) the surrogates used for marine productivity (predominantly depth in the present study) may not be linear measures of productivity; (ii) other factors in the marine environment that covary with depth (e.g. light and temperature) might have a stronger influence on species richness than productivity; (iii) the unimodal shape might be the consequence of a random process (i.e. the mid-domain effect); and (iv) seasonal pulses of productivity in shallow water might depress species richness in shallow seas. Additionally, all marine studies

consisted of poikilotherms and these have faster metabolic rates in warmer regions (Gilloooly et al., 2001). The influence of metabolic rates has been implicated in elevated rates of micro-evolution under two hypotheses (see discussions below *5.8.4 Metabolic theory of ecology*; *5.8.5 Evolutionary speed hypothesis*). Both of these hypotheses predict a positive relationship between temperature and/or productivity, suggesting a potential explanation for observed positive A–PSRRs in marine studies.

(i) Depth as a surrogate

Among the marine studies used in the present study, depth was the most commonly used surrogate (62% of the studies), and the surrogate that produced the highest proportion of hump-shaped relationships in the entire dataset (61.5%). Only one hump-shaped relationship was from a study that did not use depth as a surrogate (Wollenburg & Kuhnt, 2000). Therefore, considering the contrast with the rest of the dataset, an important question is: does productivity decline linearly with depth? The largest proportion of organic carbon in oceans comes from sea-surface primary production (Johnson et al., 2007) and deep ocean communities, particularly the benthos, are reliant on this sinking photo-detritus or particulate organic matter (POC) flux as a source of energy input. The amount of POC reaching the sea floor decreases with depth and distance from the shore due to interception by deposit feeders and remineralisation (Rex, Crame, Stuart, & Clarke, 2005). Indeed, a decline in standing stock (biomass) and the number of individuals with depth has been documented (Rex et al., 2006; Wei et al., 2010), as has an increase in biomass and number of individuals with POC flux (Johnson et al., 2007). Therefore, it would appear that depth is a good proxy for productivity given both the decline in POC, biomass and number of individuals in benthic communities with increasing depth. Therefore, the relatively high frequency of

unimodal relationships in marine systems suggests that marine organisms might respond to productivity differently than terrestrial organisms. Alternatively, other factors might modify the A–PSRR in marine systems (see *(ii) Covariant factors* and *(iv) Seasonal pulses* below).

(ii) Covariant factors with depth

There are a number of variables that change with decreasing depth that may potentially influence species richness or confound the PSRR. Those of interest include light, temperature, bottom-water oxygen concentration. Area and environmental stability might be confounding factors because different components of the ocean floor differ in size.

Light and temperature—Light and temperature are somewhat interconnected and are linked to productivity and therefore cannot be considered as confounding factors. Furthermore, benthic diversity declines rapidly below the thermocline whereas temperature declines more gradually suggesting that temperature is not a strong determinant of marine benthic diversity (Rex, Crame et al., 2005).

Bottom-water oxygen—Some regions in the ocean have depressed oxygen concentrations called oxygen minimum zones (OMZs). OMZs typically occur beneath regions of upwelling, due to excess organic matter loading, and in depths of 100–1200m (Levin et al., 2001). A common consequence of low oxygen concentration is low macrofaunal diversity coupled with high dominance (i.e. few species are abundant) (Levin et al., 2001). Therefore, in some cases where depth was used as a productivity surrogate, an apparent unimodal A–PSRR might be the artefact of depressed diversity due to an OMZ in shallower water. Seasonal pulses of productivity are characteristic of

upwelling and thus consistent with the conclusions made below (see *(iv) Seasonal pulses*).

Area and stability—The abyssal plain is the largest biome on Earth (Ramirez-Llodra et al., 2010). Hessler and Sanders (1967) first suggested that the deep-sea is hyper-diverse. Sanders (1969) argued that the deep-sea has been environmentally stable over evolutionary time allowing for radiation and diversity to accumulate in these regions. Coupled with large area, stability may result in high diversity despite low carbon flux. However, whether the deep-sea is indeed hyper-diverse is controversial (e.g. Lambshead & Boucher, 2003; Ramirez-Llodra et al., 2010). The high frequency of positive (i.e. negative with increasing depth) and unimodal relationships found in the present study is not consistent with the suggestion that deep-seas are more diverse than shallow waters.

The continental shelf covers a larger area than shallow seas (Ramirez-Llodra et al., 2010). Thus higher diversity at mid-depths might be the result of larger areas of continental shelves. Importantly however, five of the nine unimodal depth–species richness relationships specifically rule out the influence of area. However area may have had an influence the other four unimodal depth–species richness relationships suggesting that an area effect cannot be discounted entirely.

(iii) The mid-domain effect

Alternatively, the unimodal depth relationship could arise from a random process. Benthic taxa have broader depth ranges at intermediate depths such that there is a greater overlap of species ranges at mid-depths (Pineda, 1993). This phenomenon has been formalised as the mid-domain effect (MDE) (Colwell & Lees, 2000). Considering the bottom of the ocean and the ocean surface as the hard boundaries between which

marine taxa can exist provides the fundamental property under which the MDE is proposed to occur. In terrestrial environments—using altitudinal and latitudinal gradients of diversity—the MDE has received mixed support, both empirically (McCain, 2003, 2004) and theoretically (Colwell, Rahbek, & Gotelli, 2004; Hawkins, Diniz-Filho, & Weis, 2005). In marine system, the MDE has failed to predict the depth–species richness distribution of gastropods, polychaetes and bivalves (McClain & Etter, 2005) or deep-sea fishes (Kendall & Haedrich, 2006). Furthermore, in a review of studies that have tested the MDE, Zapata et al. (2003) found little support for the MDE. Thus, it is unclear whether the unimodal depth–species richness relationships can be explained by the MDE in the present study. Further, the MDE makes specific predictions about the position of the peak and the height of the peak, not just that a peak exists (Colwell & Lees, 2000). Therefore, testing for each individual relationship is required to confirm the MDE. Nonetheless, the MDE might provide a potential explanation for observed predominance of unimodal relationships in marine studies along a depth gradient.

(iv) Seasonal pulses

The decline in marine species richness with increasing depth from the bathyal zone (1000–4000m) to the abyss (> 4000m) can be attributed to the Allee effect (Rex, 1973); low population densities, resulting from low food availability, limit per capita growth rates increasing the chances of local extinction. Furthermore, few species of molluscs are entirely abyssal and species ranges are predominantly bathyal (Rex, McClain et al., 2005). Therefore, there is a source–sink dynamic between bathyal and abyssal zones. This decline in richness with increasing depth from the bathyal to the abyssal zone shows a positive relationship with productivity. However, the increase in species

richness from the photic zone to the bathyal shows an inverse relationship with productivity. Despite having higher rates of carbon flux on the upper slope (0–1000m), Rex, Crame et al. (2005) suggest that nutrient supply is more temporally variable because of pulsed, seasonal phytoplankton-blooms. High productivity pulses result in periodic rapid population growth which might limit diversity through competitive exclusion and the potential inability of predators to diversify because of low prey diversity (Rex, 1983). Furthermore, Levin and Gage (1998) found that dominance among benthic macrofauna increased with increasing sediment POC concentration. Rex, Crame et al. (2005) point out that there are no direct tests of this hypothesis. However, they do demonstrate that low diversity and high abundances are commonly observed in regions where the deep-sea benthos is subject to seasonal productivity pulses. Therefore, the depressed diversity on the upper slope may be influenced by seasonal pulses and competitive exclusion when productivity is high. However, it is important to note that the ocean is a dynamic system and the communities within it are influenced by numerous environmental factors. Furthermore, despite the species richness– depth/productivity relationship appearing at least somewhat consistent with the MDE, there are many other factors that can mediate the SPRR (e.g. habitat heterogeneity and disturbance) (Levin et al., 2001).

5.7 Relationships in homeotherms and poikilotherms

5.7.1 Homeotherms

The predominantly positive PSRRs found for homeotherms in the present study can be explained across small and large scales. Homeotherms require constant energy input to maintain the high metabolic rate needed for a constant body temperature. The 'cost of living' for terrestrial homeotherms is significantly higher than for terrestrial

poikilotherms in terms of energy requirements (Nagy, 1987). Across small scales, low levels of productivity might limit homeotherms species richness simply due to low availability of food sources and their high energy requirements for thermoregulation. As resources increase with productivity, diversity will inevitably increase (Rosenzweig & Abramsky, 1993). However, Rosenzweig and Abramsky (1993) suggest that at high levels of productivity, species richness declines. The results presented here contradict the prediction of unimodal ubiquity.

Across large scales, positive homeotherm PSRRs can potentially be explained by differential rates of molecular evolution, provided rates of molecular evolution positively affect net diversification rates (e.g. Lancaster, 2010). Colder regions are generally less productive and maintaining high metabolic rates to produce sufficient endogenous heat requires high food intake (Geiser, 2004). Furthermore, resources are relatively scarce in low productivity environments. Temperate homeotherms often undergo torpor or hibernation which can slow annual metabolic rates (McKechnie & Lovegrove, 2002). Slowed annual metabolic rates could theoretically contribute to slower rates of molecular evolution in comparison to warmer, more productive environments although this has not been directly tested (Gillman et al., 2009; Gillman & Wright, 2007). Notably, Lanfear et al. (2010) found net diversification rates in bird families correlated positively with mutation rates. Also, mammals have been demonstrated to have higher rates of DNA substitution in warmer more productive environments (Gillman et al., 2009) fitting this prediction. Additionally, Gillman et al. (2009) proposed that the red-queen hypothesis might contribute to faster rates of molecular evolution in mammals indirectly related to thermal regimes (see *5.6.5 Evolutionary speed hypothesis*).

5.7.2 Poikilotherms

Positive relationships were the most common form of the A–PSRR observed among poikilotherms. Greater productivity is generally linked to higher temperatures. Some terrestrial poikilotherms are heliothermic (e.g. lizards) requiring an external heat source to remain active. Therefore, terrestrial heliotherm diversity might be expected to be high in warmer areas. Indeed, heliotherms are often diverse in hot, but also dry places (i.e. deserts) (Powney et al., 2010; Schall & Pianka, 1978). Deserts typically have relatively low productivity suggesting that heliotherms might show a negative relationship with productivity if a broad range of productivity were considered. However, of the five studies considering terrestrial heliotherms, only one A–PSRR was negative, one was weakly unimodal, one was a relatively weakly u-shaped and the rest were positive. Importantly, all the terrestrial poikilotherm studies covered broad productivity regimes across regional and continental-to-global scales.

Higher temperatures cause faster metabolic rates in poikilotherms (Gillooly et al., 2001). The metabolic theory of ecology (MTE; see *5.8.4 Metabolic theory of ecology*) predicts a positive relationship between temperature and species richness of poikilotherms (Brown, Gillooly, Allen, Savage, & West, 2004). However, despite positive relationships being predominant, unimodal relationships were more common in poikilotherms than homeotherms suggesting that the MTE cannot be applied as a general explanation for poikilotherm PSRRs. However, temperature might not vary sufficiently in all the cases presented in the present study for the processes described by the MTE to have an influence on richness. This is particularly important across small scales where variables other than climate and productivity are more important determinants of species richness (e.g. habitat heterogeneity and area) (Field et al., 2009).

5.8 Theories to explain the observed A–PSRRs

5.8.1 Competitive exclusion

Competitive exclusion is proposed to explain unimodal PSRRs. However, unimodal relationships were less common than positive relationships across the whole dataset and in all categorical breakdowns of the A–PSRR, except marine ecosystems. Unimodal relationships were however consistently the second most frequent form of the A–PSRR. Moreover, decelerating positive relationships were only marginally less common than monotonic positive A–PSRRs at the local-to-landscape scale. After collapsing decelerating positives into unimodal relationships, unimodal relationships became the most common form of the A–PSRR at the local-to-landscape scale. However, there is no objective justification for classifying decelerating relationships as unimodal relationships when there is no evidence of a downturn in the data.

The observation of positive PSRRs at large scales is thought to be the result of unimodal relationships at small scales containing higher beta-diversity with increasing productivity (VanderMeulen et al., 2001; Whittaker et al., 2001). Therefore, it is important to explain potential mechanisms that might result in hump-shaped and similar decelerating positive A–PSRRs. Competitive exclusion predicts a hump-shaped relationship between species richness and productivity (Grime, 1973). At low productivities species richness is constrained by the amount of available resources and energy. As productivity increases conditions for life become more favourable and species richness increases. However, above a particular level of productivity, competition for resources becomes intense and poor competitors are excluded, resulting in low species richness in high productivity regimes (Grime, 1973). Alternatively, resources are proposed to be less heterogeneous in high productivity regions because plants tend to be smaller in less productive environments (Tilman, 1982; Tilman &

Pacala, 1993). This theory could explain small-scale unimodal and the similar decelerating positive A–PSRRs. Decelerating positive relationships might be the result of incomplete sampling of the entire range of productivity within a relationship that is actually unimodal. Alternatively, other factors might reduce the influence of competition as productivity increases.

5.8.2 Species pool hypothesis

The species present in any given area are a sample of the regional species pool. The species pool hypothesis proposes that more species are likely to occur in habitats or environmental conditions that are older or larger (Schamp, Laird, & Aarssen, 2002; Taylor, Aarssen, & Loehle, 1990). Taylor (1990) presented this idea as an alternative explanation for unimodal PSRRs suggesting that highly productive environments are relatively rare, small and young. Thus, these areas of high productivity have low species richness as a result of smaller area and comparatively less evolutionary time for species to adapt to the conditions than more common, older environments (Schamp et al., 2002). Gillman and Wright (2006) also point out that these less common areas are likely to be isolated from each other thus reducing the chance of colonisation from similarly small, rare, productive environments. The species pool hypothesis might therefore be a possible explanation for decelerating and hump-shaped A–PSRRs at the local-to-landscape scale. Positive A–PSRRs can also be explained by the species pool effect if the habitat sampled is predominantly in a high productivity regime. Pärtel et al. (2007) hypothesised that positive plant–PSRRs would be more common at low latitudes, and that unimodal relationships would predominate at high latitudes based on the species pool effect. At high latitudes highly productive environments are less common (in space and evolutionary time) than in the tropics. Therefore, the species pool for highly

productive areas is lower in temperate zones. Their results were consistent with this prediction. However, their review suffered from severe limitations (see *1.4. Critical analysis of PSRR reviews*) and this hypothesis remains to be tested adequately.

5.8.3 More individuals hypothesis

The more individuals hypothesis (MIH) posits that higher energy regimes can support more individuals in the ecosystem. Therefore more species, with minimum viable populations can be accommodated in the system (Wright, 1983). This hypothesis might therefore explain positive A–PSRRs. The MIH has been tested experimentally and observationally but results were equivocal (Hurlbert, 2004; Mönkkönen et al., 2006; Srivastava & Lawton, 1998; Yee & Juliano, 2007). Srivastava and Lawton (1998) controlled productivity (leaf litter) in tree holes and found that species richness of detritivorous insects was higher in holes with higher leaf litter volumes. However, the number of individuals of all species was not higher in the more productive tree holes. More recently, however, Yee and Juliano (2007) found support for the MIH with total abundances, individual species abundances, and species richness all increasing with productivity in artificial tree holes. This suggests that the MIH might be applicable at small scales. Across broader scales however, the MIH is not well supported. Tropical bird richness has been reported to be 4–5 times higher than temperate bird species richness, despite comparable abundances (Terborgh et al., 1990) indicating smaller rather than equivalent tropical population sizes. Hence, the evolutionary patterns underpinning broad-scale patterns of species richness appear to be more complex than a simple more-individuals effect. Currie et al. (2004) also point out that across broad scales species richness and abundance, and abundance and productivity are not

generally related. Therefore, the predominance of positive A–PSRRs reported here is not likely to be explained by the MIH.

5.8.4 Metabolic theory of ecology

The metabolic theory of ecology (MTE) suggests that metabolic rate is the underlying, fundamental control of observed patterns in ecology (Brown et al., 2004). Early formulations of the MTE were concerned with the effect of temperature on the metabolic rates of ectotherms (i.e. higher in warmer temperatures, Gillooly et al., 2001). However, this can only be applied to poikilotherms because homeotherms maintain a relatively constant body temperature regardless of the ambient temperatures of the environment. Nonetheless, in poikilotherms, the rate of molecular evolution scales with metabolic rate (i.e. faster molecular evolution in warmer environments) (Gillooly, Allen, West, & Brown, 2005). The proposed implications of this scaling are that faster rates of molecular evolution increase speciation rates. Therefore, warmer environments (often more productive such as the tropics) will have higher rates of speciation than cooler regions thus resulting in a greater accumulation of species in the warmer areas. This theory might then explain broad-scale, positive A–PSRRs. However, small-scale positive patterns are not likely to be explained by the MTE. Firstly, temperature is not likely to vary enough over small extents, and secondly, ecological factors unrelated to temperature generally have stronger relationships with diversity at small scales (Field et al., 2009). Moreover, MTE can only be applied to poikilotherms given that resting metabolic rates of homeotherms is independent of temperature (Mittelbach et al., 2007). However, homeotherms species richness has a similarly positive relationship with productivity.

5.8.5 Evolutionary speed hypothesis

The evolutionary speed hypothesis (ESH) posits that rates of evolution are faster in warmer environments resulting in elevated rates of speciation and an accumulation of species in these environments (Rohde, 1992). Three underlying factors are proposed for the ESH: (1) mutagenesis is elevated in warmer environments; (2) generation times are shorter in warmer environments; (3) together, higher rates of mutagenesis and shorter generation times contribute to accelerated rates of selection (Rohde, 1992). The first factor is generally applied to poikilotherms since temperature raises metabolic rates (Gillooly et al., 2001), and higher metabolic rates are thought to increase mutation rates via faster cell division and potential germline replication error, and/or the production of mtDNA damaging oxygen free radicals (Martin & Palumbi, 1993). Homeotherms on the other hand, maintain a constant body temperature and relatively constant metabolic rate suggesting that ambient temperature is less likely to affect DNA mutation rate. Therefore, it has been suggested that rates of microevolution in poikilotherms is influenced by temperature, but not in homeotherms (Mittelbach et al., 2007). This however, does not appear to be the case, with rates of microevolution being found to proceed faster in warmer climates for ectotherms (Allen et al., 2006; Wright et al., 2010; Wright et al., 2006; Wright et al., 2011) and homeotherms (Gillman et al., 2009). Importantly, Rohde (1992) expressly dismissed the influence of productivity because theory at the time suggested that the relationship between species richness and productivity was unimodal (Rosenzweig, 1992).

Recently however, a modification to ESH was proposed that implicated productivity, not temperature alone, as a driver of evolutionary speed (Gillman & Wright, 2006; Gillman & Wright, 2007; Goldie et al., 2010; Wright et al., 2006). Furthermore, Goldie et al. (2010) demonstrated that Australian woody plants in wetter

more productive regions have elevated rates of DNA evolution, consistent with this modification to the ESH. However, after controlling for body size, Lanfear et al. (2007) demonstrated that metabolic rates do not scale with mutation rates. This suggests that while the relationship between temperature and/or productivity appears to exist, the mechanism that has been proposed to accelerate micro-evolution in warmer, more productive places is not clear. Nonetheless, mutations may arise from other means in warmer environments, or may be related to annual metabolic rather than resting metabolic rate (Gillman et al., 2009). Higher annual metabolic rates might result in elevated rates of micro-evolution in regions where species do not undergo torpor. Further investigation of mechanisms that might drive micro-evolution in homeotherms is required.

Homeotherm micro-evolution might be faster in warmer environments independent of metabolic rate. An explanation for why homeotherms might have differential rates of microevolution independent of elevated rates of mutagenesis, and indirectly related to productivity, is the red-queen hypothesis (Van Valen, 1973). This explanation was proposed by Gillman et al. (2009) to potentially account for faster rates of mammal microevolution in warmer environments. The red-queen hypothesis proposes an arms race between competing species, and specifically predators and prey. If rates of microevolution among poikilotherm prey species (e.g. plants or insects) are faster in warmer environments (i.e. the ESH), they might be likely to evolve defences rapidly. Thus, in order to remain successful, predators must evolve counter defences. That means, mutations arising in a predator in an environment in which the prey are evolving defences rapidly have a greater likelihood of being beneficial than if it arose in a less competitive environment. The ESH and the accompanying red-queen hypothesis provide a plausible explanation for the predominance of positive relationships at the

continental-to-global extent but, as Gillman and Wright (2006) point out, productivity is unlikely to vary at smaller scales enough to influence rates of evolution.

CONCLUSION

The predominance of positive relationships reported in the present study contrast substantially with both the prediction that unimodal relationships are the most common form of the A–PSRR, and with a previous review (Mittelbach et al., 2001) that suggested no single form of the A–PSRR was dominant. Scale did not have a strong influence on the form of the A–PSRR and at all geographical extents and sampling grains positive relationships were the most common relationship. Again this contrasts with current scientific opinion that the relationship is highly dependent on scale. Ecosystem type did influence the form of the A–PSRR with unimodal relationships being more common than positive relationships in marine ecosystems. The contrasting pattern found in marine systems could be attributed to a random process (i.e. the MDE), a potential area effect, or the influence of other factors that mediate the PSRR. The contrast between the results of the present study and the previous review by Mittelbach et al. (2001) can be attributed to the different methods used for classifying the form of the A–PSRR. Importantly, the methods used by the previous review had a systematic bias towards unimodal relationships. A potential theoretical explanation for the predominance of positive relationships is variable rates of molecular evolution, such that species in warmer more productive regions might evolve and diversify faster. The metabolic theory of ecology might explain positive relationships in poikilotherms but not homeotherms. The evolutionary speed hypothesis, on the other hand, can potentially explain positive relationships in homeo- and poikilotherms through the direct influence of energy and metabolic rates, or indirectly via the red queen hypothesis. At smaller scales, competitive exclusion might explain unimodal and decelerating positive A–

PSRRs. Additionally, the species pool hypothesis could explain positive, decelerating

positive and unimodal relationships at small scales.

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APPENDICES

Appendix 1. Studies deemed inadmissible for testing the A–PSRR, and reasons for exclusion. Studies with sample sizes < 10 are not shown. (N = 247)

Reference	Taxa	Vert/ Invert[*]	Thermy[¶]	System[‡]	Surrogate[§]	Extent[†]	Grain[‡‡]	Reasons for exclusion and comments
Alimov 2002 a & b	a)Zooplankton b) Benthic invertebrates	I	P	A	Primary production	?	?	*Some sample sites were reservoirs or power station cooling ponds indicating anthropogenic influence
Ambrose et al. 2009	Polycheata	I	P	M	Benthic pigment concentration	R	F	*The single, instantaneous measurement of benthic pigments used is not likely to be a good estimate of the annual productivity of the sampling sites (Ambrose et al 2009)
Bachelet et al. 1996	Macro invertebrates	I	P	M	Biomass	L	?	*Unequal sampling (i.e. smaller samples at shallower depths)
Badgley and Fox 2000	Mammals	V	H	T	AET	C	C	*Other studies analysed mammal richness in North America (e.g. Currie, 1991 and Kilpatrick et al 2006)
Barbour and Brown 1974	Fish	V	P	A	Latitude	C	C	*Authors note that species richness is subject to sources of error since data is collated from published records e.g. the African lakes were known to be poorly sampled*Controlled for area *Non-normal residuals (p<0.01)
Bárcena et al. 2004	Birds	V	H	A	AET	C	C	*Breeding species richness *The study areas were characterised by short summers and harsh, long winters. Therefore, an annual measure of AET is not appropriate as a measure of productivity for breeding birds

Reference	Taxa	Vert/ Invert[*]	Thermy[¶]	System[‡]	Surrogate[§]	Extent[†]	Grain[‡‡]	Reasons for exclusion and comments
Beaver and Crisman 1989	Ciliated Protozoa	I	P	A	Trophic Status	R	?	*Trophic status is not a valid productivity surrogate since it is very likely that the nutrient input has an anthropogenic component *No statistical regression model can be fitted to the data since trophic state is categorical
Bianchelli et al. 2010	Mieofauna	I	P	M	Biopolymeric carbon	R	F	*Diversity measure is not explicit (i.e. richness of taxa)
Blake and Narayanaswamy 2004	Benthic infauna	I	P	M	Depth	R	F	*Unequal sampling. The authors also point out that the sites were under sampled
Blamires et al. 2007	Birds	V	H	T	AET	R	C	*Only the partial regression coefficient was reported making the determination of the form of the relationship difficult
Bonn et al. 2004	Birds	V	H	?	NDVI	R	C	*Number of species per grid cell was measured as well as number of species per NDVI class. After controlling for area, both had a positive relationship *The species richness data source is the same source used by van Rensburg et al (2002) who used a direct measure of productivity (NPP)
Braschler et al. 2004 a & b	a)Grasshoppers b) Gastropods	I	P	T	Above-ground plant biomass	L	F	*The area has been substantially modified from beech forest to grassland for cattle grazing
Brown and Davidson 1977	Rodents	V	H	T	Annual Rainfall	C	F	*Data were duplicated from another study already included in the analysis (Brown, 1973)
Chase and Ryberg 2004	Animals	V/I	P	A	Algal biomass accrual	?	?	*Less connected data was reported in Chase and Leibold (2002)

Reference	Taxa	Vert/ Invert[*]	Thermy[¶]	System[‡]	Surrogate[§]	Extent[†]	Grain[‡‡]	Reasons for exclusion and comments
Chown and Gaston 1999	Procellariiform birds	V	H	M	Chl a	C	C	*The highest productivity sites were seasonally variable and small
Chown et al. 2003	Birds	V	H	T	NPP	R	C	*Same data as van Rensburg et al. (2002)
Cook 1969	Birds	V	H	?	Latitude	C	C	* The data almost certainly shows a positive relationship but, the data were categorical making regression impossible
Corliss et al. 2009	Benthic foraminifera	I	P	M	Sea Surface Productivity	C	F	*Two sampling units were used *The residuals are not normally distributed (p>0.1)
Cosson-Sarradin et al. 1998	Polycheata	I	P	M	Est. Primary Productivity	R	C	*The eutrophic site consisted of 4 samples, whereas the oligotrophic and mesotrophic sites consisted of 5 samples; therefore, sampling regime varied by more than 10% *Additional data used for analyses was from another study that used a different sampling method (i.e. smaller sampling unit)
Currie 1991 a & b	a) Birds b) Mammals	V	H	T	Primary Production	C	C	a) A newer dataset was used by Hurlbert and Haskell (2003) for North American birds b) The data is not evenly distributed and a single relationship cannot be determined
Daniels et al. 1992	Amphibians	V	P	?	Latitude	R	C	*Parts of the sample area were significantly influenced by human activities * Non-normal residuals
Davidowitz and Rosenzweig 1998	Grasshoppers	I	P	T	Latitude	C	C	*The group studied are predominantly adapted to feeding of grass and, the hump portion of the curve occurs in areas dominated by grass prairies. Thus, the hump-shape is a result of available habitat, not productivity *Too taxonomically restrictive

Reference	Taxa	Vert/ Invert[*]	Thermy[¶]	System[‡]	Surrogate[§]	Extent[†]	Grain[‡‡]	Reasons for exclusion and comments
Davies et al. 2007a	Birds	V	H	A/T	NDVI	C	C	*The study presents multi-variable models and data was not re-analysed *Spatial GLS regression model *There is no figure available in order to determine the form *Storch et al (2006) also analysed global bird richness
Davies et al. 2007b	Parrots	V	H	T	NPP	C	C	*It is difficult to determine the forms of the relationships with no figure
Davis et al. 2008	Dung Beetles	I	P	T	Rainfall	R	C	*The sample sites were on livestock farms
Dean 2000	Birds	V	H	T	Rainfall	R	C	*Large portions of the Karoo are grazed by domestic livestock
Death 1995	Benthic Invertebrate	I	P	A	Epilithic Carbon	L	?	*Mean values from Death and Winterbourne (1995)
De'ath and Fabricus 2010 a–c	a) Hard corals b)Phototrophic octocorals c)Heterotrophic octocorals	I	P	M	Chl a	R	C	*The study assessed the influence of water quality on reef health *Nutrient input is largely a result of anthropogenic activity in the catchments of inflow rivers
Declerck et al. 2005 a–f	a) Rotifers b) Copepods c) Cladocerans d) Macro invertebrates e) Fish f) Rotifers	a) I b) I c) I d) I e) V f) I	P	A	Total phosphorous	R	C	*Residuals of TP and richness controlling for area and submerged macrophyte cover *Declerck et al (2005) used a significance level of $p < 0.1$ *Much of the nutrient input is from anthropogenic sources
Diniz-Filho et al. 2004	Birds (Owls)	V	H	T	AET	C	C	*Data were not obtained and no figure is published making it difficult to determine the form of the relationship

Reference	Taxa	Vert/ Invert[*]	Thermy[¶]	System[‡]	Surrogate[§]	Extent[†]	Grain[‡‡]	Reasons for exclusion and comments
Diniz-Filho et al. 2008 a–d	a) Mammals b) Birds c) Reptiles d) Amphibians	V	H	T	AET	R	C	*There was a significant positive relationship between AET and species richness in multiple regression models but no simple regression coefficients are given
Dodson 2008	Zooplankton	I	P	A	Chl a	L	F	*Artificial ponds
Dodson et al. 2000 a–d	a) Rotifers b) Cladocera c) Copepods d) Fish	I	P	A	Pelagic primary production	?	?	*Three lakes are excluded due to experimental manipulation of nutrient loadings *The study includes lakes that had development in their catchments which Hoffman and Dodson (2005) showed influenced the relationship
d'Onghia et al. 2004	Fish	V	P	M	Depth	R	C	*Unequal sampling effort
Fariña et al. 1997	Benthic Decapods	I	P	M	Depth	R	?	*Only the continental shelf (100-200m) and upper slope (200-500m) were sampled suggesting that a full range of depths has not been sampled *Also the study site is characterised by seasonal upwelling (e.g. Tilstone et al 1994) indicating that depth per se does not reflect the productivity regime
Fock 2009	Pelagic ichthyonekton	I	P	M	Average annual Primary Production	C	C	*Unequal sampling effort
De Mas et al. 2009	Spiders	I	P	T	NDVI	L	F	*Unequal sampling effort
Follesa et al. 2009	Crustacea	I	P	M	Depth	L	C	*Trawl time differed between depths
Gage et al. 2004	Cumacea	I	P	M	Latitude	C	C	*Different sampling units

Reference	Taxa	Vert/ Invert[*]	Thermy[¶]	System[‡]	Surrogate[§]	Extent[†]	Grain[‡‡]	Reasons for exclusion and comments
Ganzhorn et al. 1997	Lemurs	V	H	T	Annual Rainfall	R	?	*Rainfall is a poor productivity surrogate in Madagascar considering its subtropical climate and the broad geographical variation in climate across the island
Ghilarov and Timonin 1972	Zooplankton	I	P	A	Biomass of target taxa	R	F	*The sampling regime was uneven with three of the lakes being sampled three times and the other four lakes only sampled once
Gonzales-Taboda et al. 2007	Birds	V	H	T	NDVI	R	C	*Three grains presented with no qualitative difference for all three grains. Thus the largest grain was included
Graham et al. 2009	Ants	I	P	T	NPP	L	F	*The study includes sites that have significantly modified by humans and considers the influence of disturbance i.e. intermediate disturbance hypothesis
Gutiérrez - Aguirre and Suarez-Morales 2001	Copepods	I	P	A	Transparency	L	C	*Lake side development influenced species richness. Therefore, reject due to anthropogenic influence
Haberl et al. 2005	Birds	V	H	T	NPP	R	?	*Uses human appropriation of Net Primary Production as the measure of productivity indicating strong human influence in the study area which, is not surprising in a high population density area like Austria
H-Acevedo and Currie 2003	Birds	V	H	T	NDVI	C	C	*Considering seasonal richness and seasonal NDVI a third degree polynomial fits the data. But, relationships were positive as indicated by LOWESS trend lines *Data unavailable and figure was too dense to digitise

Reference	Taxa	Vert/Invert[*]	Thermy[¶]	System[‡]	Surrogate[§]	Extent[†]	Grain[‡‡]	Reasons for exclusion and comments
Hacking 2007	Macrofauna	I	P	A/T	Biomass	R	F	*Species richness and biomass are strongly influenced by physical processes as indicated by the study. Biomass therefore does not represent a valid surrogate
Hawkins 2004	Birds	V	H	T	Summer GVI	C	C	*Summer GVI was used rather than annual GVI since breeding richness was measured *A positive relationship is favoured because there is no downturn at high GVI levels *Qualitatively similar to Hurlbert and Haskell (2003)
Hawkins and Porter 2003	Butterflies	I	P	T	AET	C	C	*Richness data from Kudrna (2002) *Qualitatively indifferent from above
Hawkins et al. 2003	Birds	V	H	T	AET	C	C	*The data was analysed as global and regional datasets. Because there is no taxonomic restriction (i.e. all terrestrial birds), the global analysis is appropriate *Storch et al 2006 also performed a global analysis of bird richness and AET for which data was available for re-analysis
Hawkins et al. 2005	Birds	V	H	T	AET	C	C	*There is no figure to determine the form of the relationship
Hawkins et al. 2007	Birds	V	H	T	AET	C	C	*Similar to Hawkins et al. (2003) and Storch et al. (2006) in that it compares global bird richness with AET
Hessen et al. 2006	Pelagic zooplankton	I	P	A	Chl a	R	F	*LOWESS curve does not turn down indicating a decreasing positive *Most lakes sampled were of low productivity not a reflecting a sufficient gradient of productivity*Some lakes were sampled more than others indicating uneven sampling

Reference	Taxa	Vert/Invert[*]	Thermy[¶]	System[‡]	Surrogate[§]	Extent[†]	Grain[‡‡]	Reasons for exclusion and comments
Hobæk et al. 2002	Crustacean zooplankton	I	P	A	Algal biovolume	R	F	*Many of the lakes are small and situated in urban or suburban surroundings, being subject to influences from eutrophication as well as introduction of alien fish species. In particular, pike (Esox lucius) was introduced in many lakes around 100–130 years ago. (Hobæk et al 2002)
Hof et al. 2008	Freshwater animals	V/I	P	A	Latitude	C	C	*Although the regions differed in size, area did not influence species richness. However, some areas were large, spanning broad latitudinal ranges. Thus, using the latitudinal midpoint is not an ideal proxy of productivity
Hoyer and Canfield 1990	Birds	V	H	A	Chl a	R	C	*Subset of Hoyer and Canfield (1994)
Hugo and van Rensburg 2008	Birds	V	H	T	NDVI	R	C	*Same data as van Rensburg et al (2002)
Huston 1985	Corals	I	P	M	Depth	?	?	*Homeosymbiont zooxanthelle in corals are reliant on light which decreases with depth. Therefore, depth reflects productivity. However, in shallower water, environmental stress is high (e.g. wave action and sedimentation) which is detrimental to coral diversity and imposes a stronger influence than depth related light intensity

Reference	Taxa	Vert/Invert[*]	Thermy[¶]	System[‡]	Surrogate[§]	Extent[†]	Grain[‡‡]	Reasons for exclusion and comments
Janzen 1981	Wasps	I	P	T	Latitude	C	?	*In the continental USA, the latitudinal range of sampling (i.e. from 70-50 degrees N) does not reflect a constant decrease in productivity with increasing latitude *Using a single family of parasitic wasps is taxonomically restrictive *Janzen (1981) states that the richness of parasitic wasps is highly dependent on host species
Jarvinen and Vaisanen 1978	Birds	V	H	A	Biomass	R	C	*Sampling regime is not constant with transects ranging between 97 and 439km
Jennings et al. 1999 a & b	a) Free living epibenthic fauna b) Attached epibenthic fauna	I	P	M	Latitude	R	C	*Commercial trawling effort was higher, and species richness was lower at low latitudes making it difficult to determine the effect of productivity using latitude
Jeppesen et al. 2000 a & b	a) Zooplankton b) Fish	a) I b) V	P	A	Total phosphorous	R	F	*Total phosphorous is not presented as continuous but as classes *Phosphorous is not a good measure of productivity since at high concentrations it causes water bodies to go eutrophic resulting in an oxygen deficit
Jetz and Rahbek 2002	Birds	V	H	?	NPP	C	C	*Relates species richness of birds with different range sizes to productivity *No figure published for all species
Jetz et al. 2009	Birds	V	H	T	AET	C	C	*R2 values obtained from Pearson correlations and relationship forms from figures *Storch et al (2006) also analysed birds species richness, but used equal area grid squares
Kaspari et al. 2000	Ants	I	P	T	Net aboveground productivity	C	C	*Species per transect *Essentially the same data as Kaspari et al (2000a) but at a different grain

Reference	Taxa	Vert/ Invert[*]	Thermy[¶]	System[‡]	Surrogate[§]	Extent[†]	Grain[‡‡]	Reasons for exclusion and comments
Kaufman and Willig 1998	Mammals	V	H	T	Latitude	C	C	*More appropriate studies using direct measures of productivity are available *Tognelli and Kelt (2004) used AET for mammals in South America
Kay et al. 1997	Primates	V	H	T	Annual Rainfall	C	?	*Rainfall is not a suitable surrogate for productivity *Data in the study shows that rainfall and productivity (indexed from litter fall) have a unimodal relationship in this particular habitat type (Figure 3 in Kay et al 1997)
Keil and Hawkins 2009 a & b	a) Butterflies b) Dragonflies	I	P	a) T b) A/T	AET	R	C	a) Same data as Hawkins and Porter (2003) b) Same data as Keil et al (2008)
Keil et al. 2008	Hoverflies	I	P	?	AET	C	C	*AET and richness values were means for whole countries *Sampling effort varies between countries
Kerr and Packer 1999	Beetles	I	P	T	NPP	C	C	*Too taxonomically restrictive (one genus of beetle)
Kerr et al. 2001	Butterflies	I	P	T	NPP	C	C	*Habitat heterogeneity and PET were stronger predictors of species richness so results of NPP vs. richness were not reported by the authors
Kilpatrick et al. 2006	Mammals	V	H	T	AET	C	C	*It was not possible to determine the form of the relationship
Kissling et al. 2009	Frugivorous birds	V	H	T	NPP	C	C	*Non-normal residuals (p<0.01) *Although the quadratic is significant, visual inspection of the relationship does not show a u-form *Storch et al (2006) analysed global bird richness. Therefore, in essence this is a subset of that data.
Klop and Prins 2008 a & b	a)Grazers b) Browsers	V	H	T	AET	R	C	*Richness was influenced by anthropogenic fires

Reference	Taxa	Vert/ Invert[*]	Thermy[¶]	System[‡]	Surrogate[§]	Extent[†]	Grain[‡‡]	Reasons for exclusion and comments
Kumschick et al. 2009a	Ants	I	P	T	NPP	R	C	*Ambient energy predicts ant richness *One of the habitat types is classified as 'arable land' suggesting human influence
Kumschick et al. 2009b	Spiders	I	P	T	Latitude	R	C	*A hump shaped relationship was predicted due to biotic interactions in lower latitudes. Therefore, biotic interactions are confounding *Taxonomically restricted *One of the habitat types is classified as 'arable land' suggesting human influence
Lambshead et al. 2000	Nematodes	I	P	M	Latitude	R	F	*Productivity increases pole wards in the North Atlantic (Campbell & Arup 1992) *Unequal sampling effort
Lambshead et al. 2002	Nematodes	I	P	M	Latitude	R	F	*Different sampling units were used but the authors argue that the results were unbiased and conservative for areas of high diversity *The data are not evenly distributed across the range of latitude (i.e. a gap between 8 and 22 degrees North)
Lassau and Hochuli 2007	Wasps	I	P	T	NDVI	R	F	*NDVI was used as a measure of habitat complexity but it is difficult to disentangle 'complexity' from productivity particularly at local scales*LOWESS line doe not curve upward at the low productivity end indicating an increasing positive
Lassau and Hochuli 2008	Beetles	I	P	T	NDVI	R	F	*NDVI was used as a measure of habitat complexity but it is difficult to disentangle 'complexity' from productivity particularly at local scales

Reference	Taxa	Vert/ Invert[*]	Thermy[¶]	System[‡]	Surrogate[§]	Extent[†]	Grain[‡‡]	Reasons for exclusion and comments
Lassau et al. 2005	Ants	I	P	T	NDVI	R	F	*NDVI was used as a measure of habitat complexity but it is difficult to disentangle 'complexity' from productivity particularly at local scales *A single point had undue influence on the quadratic model at the low productivity end
Lee et al. 2004	Birds	V	H	T	NDVI	R	C	*An accelerating positive is favoured over a U-shapes since species richness increases slightly when NDVI<0.5 and it is positive when NDVI>0.5 (Lee et al. 2004) *Some quadrats have a high proportion built up areas and species richness decreased with proportion of built up area. Thus, decreasing NDVI may only be collinear with human density which negatively influences species richness
Leibold 1999	Zooplankton	I	P	A	TP	R	F	*Four of the ponds sampled were artificial but Leibold (1999) argues that they have not been disturbed for at least eight years *However, one of the ponds is an abandoned dairy-waste settling pond that is extremely eutrophic *Removal of the pond with the highest phosphorous concentration (assumed to be the dairy-waste settlement pond) results in a non-significant relationship
Loya 1972	Corals	I	P	M	Depth	L	F	*Sampling regime is not constant ranging from 17 transects between 3m and 7m and 9 transects between 20m and 30m *Low coral richness at shallow depths is an artefact of disturbance (e.g. wave action) and not a gradient of productivity.

Reference	Taxa	Vert/ Invert[*]	Thermy[¶]	System[‡]	Surrogate[§]	Extent[†]	Grain[‡‡]	Reasons for exclusion and comments
Mahon and Mahon 1994	Fish	V	P	M	Biomass	L	?	*The sample sites (tide pools) vary in volume *The number of individuals, biomass and species richness decrease with decreasing volume *The study represents a species-area effect
Malmqvist and Eriksson 1995	Insects	I	P	A	Chl A, Seston Energy, Conductivity (PCA axis)	L	?	*Unable to obtain a full copy of the article
Maraun et al. 2007	Oribatid mites	I	P	T	Latitude	C	C	*Latitudes were estimated from the median of the country and the authors caution against strong interpretation of the results since some countries span broad latitudinal ranges
Marinone et al. 2006	Zooplankton	I	P	A	Chl a	R	F	*The study investigates the influence of ultraviolet radiation (UVR) on zooplankton communities and finds equivocal evidence that high levels of UVR in the water column can negatively influence species richness. However, lake transparency (linked to productivity) reduces UVR in the water column making it difficult to uncouple the effects
Marshall and Camp 2006	Plethodontid salamanders	V	P	A/T	PCA axis (energy)	R	C	*Rainfall but not temperature had a PCA loading suggesting PC1 may not be a surrogate for productivity and the positive relationship may be an artefact of the reliance of salamanders on water for reproduction *The quadratic term is marginally non-significant but, the relationship is a decelerating positive

Reference	Taxa	Vert/ Invert[*]	Thermy[¶]	System[‡]	Surrogate[§]	Extent[†]	Grain[‡‡]	Reasons for exclusion and comments
Mathais et al. 2004	Birds (Parrots)	V	H	T	AET	C	C	*Compared the influence of productivity using different data sources *The results using different data sources were quantitatively similar *Davies et al (2007) used one of the same data sources and used a direct measure of productivity (NPP)
McCain 2003	Rodents	V	H	T	Latitude	R	C	*Latitude does not represent a gradient of productivity
McCormick et al. 2004	Macro invertebrates	I	P	A	Phosphorous	L	F	*Enrichment is from anthropogenic sources
McPherson and Jetz 2007	Birds	V	H	T	NPP	C	C	*Although the OLS equation in the supplementary data indicates a curvilinear relationship, it is difficult to determine if the relationship is unimodal or a decelerating positive
Meserve et al. 1991	Small mammals	V	H	T	Latitude	R	F	*Unequal sampling effort
Milner et al. 2001	Macro invertebrates	I	P	A	Chl a	L	F	*Distance from glacier and temperature had a stronger influence on species richness suggesting temperature tolerance is more important
Miserendino 2009	Macro invertebrates	I	P	A	Chl a	R	F	*Anthropogenic nutrient input from urban, agriculture and livestock activities
Moore et al. 2002	Vertebrates (Birds, Mammals, Amphibians and Snakes)	V	P/H	?	NPP	C	C	*Uses the same data as Balmford et al. 2001

Reference	Taxa	Vert/ Invert[*]	Thermy[¶]	System[‡]	Surrogate[§]	Extent[†]	Grain[‡‡]	Reasons for exclusion and comments
Moreno-Rueda and Pizzaro 2007 a–d	a) Birds b) Mammals c) Reptiles d) Amphibians	V	a) H b) H c) P d) P	T	Rainfall	L	C	*On average 29.6km2 of every 100km2 square was farmland *"Water stored in subsoil is an important determinant of productivity in the study area, and it is not necessarily correlated with precipitation" (Moreno-Rueda and Pizzaro 2007) *Environmental heterogeneity was more important that climate predictors
Morton and Davidson 1988	Ants	I	P	T	Annual Rainfall	R	F	*Data duplicated from Brown and Davidson (1977a)
Narayanaswamy et al. 2005	Polychaetes	I	P	M	Depth	L	F	*Different sampling units were used due to constraints *The relationship is positive but there is a peak in diversity at 400m
Nilsson and Nilsson 1978	Birds	V	H	A	Phosphorous	R	C	*Area has a strong influence on species richness *Lakes had shoreline development indicating anthropogenic nutrient input
Obertegger et al. 2010	Rotifers	I	P	A	TP	L	C	*No single variable regression was presented between species richness and total phosphorous. In addition, given the variation in temperature along an elevational gradient, TP is not a good proxy for productivity
O'Brien et al. 2004	Zooplankton	I	P	A	Chl a	L	F	*Chlorophyll *a* had no relationship with species richness but no statistics were reported
Oindo 2002a	Herbivorous mammals	V	H	T	NDVI	R	C	*Used the landscape richness data since it uses equal area grids cells *The data is not evenly spread across the full range of productivity
Oindo 2002b	Herbivorous mammals	V	H	T	NDVI	R	C	*Uses a subset of the Oindo (2002a) data but at a different scale *Only 144 of the reported 378 data points could be digitized from the published figure. But, the results were qualitatively similar

Reference	Taxa	Vert/Invert[*]	Thermy[¶]	System[‡]	Surrogate[§]	Extent[†]	Grain[‡‡]	Reasons for exclusion and comments
Olin et al. 2002	Fish	V	P	A	Total phosphorous	L	C	*Many of the lakes have human settlements on the lake shore suggesting that enrichment has a significant anthropogenic component *Five of the study lakes have had 'mass removal' of cyprinids, and one lake has been biomanipulated
Patalas 1971	Zooplankton	I	P	A	Chl a	L	F	*Area relates positively with richness so using species-area residuals is more appropriate. *However, after controlling for area the relationship is still non-significant *The sampling regime was not held constant throughout the study. Two different sampling units were used in different years and different lakes and, four of the lakes were sampled twice and some only once
Paterson and Lambshead 1995	Nematodes	I	P	A	Depth	R	F	*The data is not evenly distributed along the range of depth (i.e. a large gap between 1800 and 2875m). Also one of the sites (2875m) was a permanent site sampled four times and mean richness calculated.
Patten 2004 a & b	a) Bats b) Birds	V	H	T	Vegetation cover	C	C	*After controlling for area, vegetation cover had no influence on richness *Vegetation cover is not a good surrogate for productivity
Pearson and Carroll 1998 a–e	North America a) Birds b) Butterflies c) Tiger beetles India d) Birds e) Tiger beetles	a) V b) I c) I d) V e) I	a) H b) P c) P d) H e) P	T	Annual Rainfall	C	?	*Rainfall is not a suitable surrogate for productivity across North America since rainfall is confounded by temperature in northern regions

Reference	Taxa	Vert/ Invert[*]	Thermy[¶]	System[‡]	Surrogate[§]	Extent[†]	Grain[‡‡]	Reasons for exclusion and comments
Peres 1997	Primates	V	H	T	Biomass	R	?	*The study compares two different forest types, terra firme and varzea (flooded for up to half the year) *The data does not reflect a productivity gradient
Peters and Traunsperer 2005	Free living nematodes	I	P	A	Chl a	L	F	*Many of the lakes have human settlements on the lake shore suggesting that enrichment has a significant anthropogenic component
Pfeiffer et al. 2003	Ants	I	P	T	Rainfall	R	C	*Narrow range of rainfall (84-197 mm/yr)
Phillips et al. 2009	Birds	V	H	T	GPP	C	C	*Digitized figure yielded 1271 compared to 1390 reported. However, qualitatively the results did not differ and, quantitatively, were almost identical *NDVI, NPP, and GPP were strongly and positively correlated *Used the same bird data used by Hurlbert and Haskell (2003)
Pianka 1967	Lizards	V	P	T	Warm Season Rainfall	R	?	*Sites visits and sampling varied (3-10 times)
Pianka 1971	Lizards	V	P	T	Annual Rainfall	R	?	*No methods for the lizard census are provided. However, methods follow Pianka (1967) closely suggesting a varied sampling regime
Pierce et al. 1994	Fish	V	P	A	Biomass	L	F	*Richness is positively related to area (p=0.007). Therefore, use species-area residuals *The lakes sampled are either in close proximity or adjacent to human settlement (e.g. Memphremagog) indicating anthropogenic influence. Galvez-Cloutier and Sanchez (2007) show that some lakes in Quebec require eutrophic control measures due to nutrient input from human activities (e.g. Lakes Waterloo and Roxton)

Reference	Taxa	Vert/Invert[*]	Thermy[¶]	System[‡]	Surrogate[§]	Extent[†]	Grain[‡‡]	Reasons for exclusion and comments
Pinto-Coelho et al. 2005	Crustacean zooplankton	I	P	A	Chl a	C	C	*Unequal sampling effort and methods
Porter 1972	Corals	I	P	M	Depth	L	?	*In shallower water, environmental stress is high (e.g. wave action and sedimentation) which is detrimental to coral diversity and imposes a stronger influence than depth related light intensity
Price et al. 1998	Gall Insects	I	P	T	Latitude	C	?	*Sampling regime is not constant with Arizona and Minas Gerias sampled "intensively" and "intermittently everywhere else" (Price et al. 1998, p. 582) *Also for a global study no sites in tropical Africa were sampled and only one site in the tropical Pacific was sampled
Priede et al. 2010	Fish	V	P	M	Depth	R	C	*Unequal sampling effort
Qian 2008	Birds	V	H	T	AET	C	C	*Multiple regression results including a quadratic term for AET were presented, but without a figure it is impossible to determine if the relationship is a decreasing positive or unimodal *Storch et al 2006 also did a global analysis of birds and AET
Qian 2010 a–d	a) Mammals b) Birds c) Amphibians d) Reptiles	V	a) H b) H c) P d) P	T	AET	C	C	*No figure or regression coefficients available for global analysis
Randall and Minns 2002	Fish	V	P	A	Habitat Productivity Index	R	F	*Unequal sampling effort
Rangel and Diniz-Filho 2003	Birds: Falconiformes (Global)	V	H	T	NPP (class)	C	C	*No data or figure available *The measure of NPP was crude (i.e. categorical)

Reference	Taxa	Vert/ Invert[*]	Thermy[¶]	System[‡]	Surrogate[§]	Extent[†]	Grain[‡‡]	Reasons for exclusion and comments
Rangel and Diniz-Filho 2004 a–e	Birds: Falconiformes a) Eurasia b) Africa c) Australia d) Neartic e) Neotropics	V	H	T	NPP (class)	C	C	*No data or figure available *The measure of NPP was crude (i.e. categorical) *Results were obtained through spatial analysis
Rebelo 1992	Fish	V	P	M	Biomass	L	?	*The watershed of the lagoon has a number of anthropogenic inputs including paper-pulp factories, urban sewerage and cattle effluent
Reed and Fleagle 1995 a–d	Primates a) Asia b) South America c) Africa d) Madagascar	V	H	T	Annual Rainfall	C	?	*The authors suggest that area in confounding since Asia contains many islands therefore constraining diversity independently from rainfall *Also Asia is subject to monsoonal climates suggesting that productivity is not strongly influenced by rainfall at an annual scale **Rainfall is not a precise estimate of productivity in tropical rainforests
Reed et al. 2006	Rodents	V	H	T	Rainfall	R	?	*A portion of the data was taken from a study already reported (Brown 1973)
Renaud et al. 2006	Benthic Macrofauna	I	P	M	Depth	R	F	*The taxon classification is too course and non-specific
Rombouts et al. 2009	Copepods	I	P	M	Chl a	C	C	*Unequal sampling effort
Rompré et al. 2007	Birds	V	H	T	Rainfall	L	C	*Constant, high temperature suggests rainfall is appropriate surrogate *Much of the forest is fragmented from human activity
Rossetti et al. 2009	Rotifers	I	P	A	Chl a	L	F	*The river basin is densely inhabited, and contains a high proportion of agricultural land and industrial activity

Reference	Taxa	Vert/ Invert[*]	Thermy[¶]	System[‡]	Surrogate[§]	Extent[†]	Grain[‡‡]	Reasons for exclusion and comments
Rowhani et al. 2008	Birds	V	H	?	EVI	C	C	*Used the same bird data as Hurlbert and Haskell (2003)
Roy et al. 1998	Gastropoda	I	P	M	Sea Surface Temperature	?	?	*Sea surface temperature is not a good surrogate for productivity. Marine productivity is complex and influenced by more than just ambient energy (Kaustuv Roy, personal communication)
Ruggiero 1999	Mammals	V	H	T	NPP	C	C	*The original study analyses were based on 170 grid cells but, using data points digitised from the figure only 85 were obtained *Same data as Ruggiero and Kitzberger 2004
Ruggiero and Kitzberger 2004	Mammals	V	H	T	AET	C	C	*Same data as Ruggiero (1999)
Sajan et al. 2010	Nematodes	I	P	M	Depth	R	F	*The depth range covers 188 meters yet there is a large gap of 73 meters between 123 and 196 meters, almost a third of the entire depth range
Sandin et al. 2008	Fish	V	P	M	Chl a	R	C	*It is difficult to separate the influence of productivity from the influence of reef isolation.
Scheibe 1987	Lizards	V	P	T	Warm Season Rainfall	R	?	*The is a large variation in altitude between sites (310-2290m), and a correlation matrix identifies that altitude has a positive and negative relationship with precipitation (cold and warm season) and temperature (January and July) respectively *Rainfall is therefore confounded by altitude
Schrag et al. 2009	Birds	V	H	T	NDVI	R	C	*A large proportion of study sites consisted of annual croplands and pasture
Schratzberger and Rogers 2006	Nematodes	I	P	M	Depth	R	F	*Three of the 19 sample sites consisted of two, not three replicates. Analysis without the these three sites yielded qualitatively similar results

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Reference	Taxa	Vert/Invert[*]	Thermy[¶]	System[‡]	Surrogate[§]	Extent[†]	Grain[‡‡]	Reasons for exclusion and comments
Sellanes et al. 2010 a & b	a) Macrofauna b) Megafauna	I	P	M	Chloroplastic pigments	R	C	*Same data as Quiroga et al (2009)
Seto et al. 2004 a & b	a) Birds b) Butterflies	a) V b) I	a) H b) P	T	summer NDVI	L	C	*Same data as Bailey et al 2004
Shanker and Sukumar 1998	Mammals	V	H	T	Biomass	?	?	*The majority of the areas surrounding sample sites are dominated by exotic plantation species
Sheftel and Hanski 2002	Shrews	V	H	T	Pooled abundance	R	F	*Density of shrews correlates with food resource availability *Too taxonomically restrictive (i.e. single genus)
Shepherd 1998	Mammals	V	H	T	Latitude	C	?	*The study sites do not reflect a gradient in productivity since site the study sites between 30 and 40 degrees are in areas of low productivity relative to some more northerly sites
Sheppard 1980	Corals	I	P	M	Depth	?	?	*The author suggests that the 20m peak in diversity results from protection from extreme weather, high turbulence and not influenced by silt-laden upwelling and cold currents
Simpson et al. 1986	Benthic Invertebrate	I	P	A	Biomass	L	?	*The Hudson River flows through industrial and commercial areas suggesting anthropogenic input. In the past large quantities of PCBs have been discharged into the waterway up river of the sample sites.
Standen 1979	Earthworms	I	P	T	Annual Rainfall	L	?	*Rainfall is not a reflection of productivity in the habitats sampled (i.e. high rainfall, low temperatures). In addition, rainfall is confounded by elevation.
Stuart and Rex 2009	Gastropods	I	P	M	Depth	?	C	*Unequal sampling effort
Szarek et al. 2009	Foramifera	I	P	M	Carbon flux	R	F	*Three different sampling devices were used

Reference	Taxa	Vert/ Invert[*]	Thermy[¶]	System[‡]	Surrogate[§]	Extent[†]	Grain[‡‡]	Reasons for exclusion and comments
Takamura et al. 2009	Macro invertebrates	I	P	A	Chl a	L	F	*Chlorophyll concentration alone does not reflect productivity in the lake since macrophytes capture some of the nutrients in the water column
Tales and Berrebi 2007	Fish	V	P	A	Chl a	L	C	*The reach of river sampled is between two weirs and the river bank is lined with either human settlements or farmland
Tedesco et al. 2005	Fish	V	P	A	NPP	C	C	*Area has a strong influence on species richness but, after controlling for area there is no relationship with productivity *Tedesco et al (2005) suggest that productivity does not vary enough between study sites for productivity to have a visible effect. Thus, a non-significant relationship is unsurprising
Tello and Stevens 2010	Bats	V	H	T	NPP, annual-precipitation and temperature	C	C	*Energy was considered as a combined model containing rainfall and temperature in addition to NPP. Only the R^2 value was reported making it difficult to determine the form of the relationship
Terribile and Diniz-Filho 2009	Coral snakes	V	P	T	NPP	C	C	*Too taxonomically restrictive being a clade in a single family
Terribile et al. 2009 a & b	Snakes a) Elapidae b) Viperidae	V	P	T	AET	C	C	*Too taxonomically restrictive being only a single family *Analysed by region to reduce effect of history *Did not analyse the squares where species richness was zero

Reference	Taxa	Vert/Invert[*]	Thermy[¶]	System[‡]	Surrogate[§]	Extent[†]	Grain[‡‡]	Reasons for exclusion and comments
Thomas and MacLean 1988	Mites	I	P	T	Mite biomass	R	?	*Two of the sites (part of a triplicate) were influenced by an oil spill and one sites was burned *The majority of sites were replicates with one taken in the wet and the other in the dry season. Therefore, the study does not represent spatial variation in diversity
Tolonen et al. 2005a	a) Benthic Macro invertebrates b) Zooplankton	I	P	A	TP	L	F	*One third of the sites had nutrient loading from treated sewage and discharge from a pulp mill
Werner et al. 2007	Amphibians	V	P	A	Proportion canopy cover	L	F	*Canopy cover is a poor measure of productivity across such a small scale (525 hectares)
White and Hurlbert 2010	Birds	V	H	T	NDVI	C	C	*Same data as Hurlbert and Haskell (2003)
Whiteside and Harmsworth 1967	Cladocera	I	P	A	Phytoplankton Production	L	?	*The data is not evenly distributed along the range of productivity (i.e. a large gap between 800 and 1400 g/m2 year)
Wlodarska-Kowalczuk et al. 2004	Benthic Macrofauna	I	P	M	Depth	L	F	*Unequal sampling effort
Yom-Tov and Werner 1996 a–c	a) Birds b) Mammals c) Reptiles	V	H	T	Rainfall	R	C	*Unequal sampling effort
Zhao et al. 2006a	Birds	V	H	T	NPP	C	C	*Qian et al 2009 also analysed birds in China
Zhao et al. 2006b	Amphibians	V	P	A/T	NPP	C	C	* R^2 and p-value taken from supplementary data *Qian et al (2007) was more extensive.

Reference	Taxa	Vert/Invert[*]	Thermy[¶]	System[‡]	Surrogate[§]	Extent[†]	Grain[‡‡]	Reasons for exclusion and comments
Zhao et al. 2006c	Reptiles	V	P	T	NPP	C	C	*R^2 and *p*-value taken from supplementary data *Qian et al (2007) was more extensive

*Vert/Invert: V, vertebrate; I, invertebrate; V/I, both

¶ Thermy: H, homeotherm; P, poikilotherm

‡System: T, terrestrial; A, freshwater aquatic; M, marine; A/T, freshwater aquatic and terrestrial

§Surrogate: NPP, net primary production; GPP, gross primary production; AET, actual evapotranspiration; PET, potential evapotranspiration; NDVI, normalized difference vegetation index; EVI, enhanced vegetation index; GVI, global vegetation index; TP, total phosphorous; Chl a, chlorophyll *a* concentration

†Extent: L, local-to-landscape (0–200km); R, regional (200–4000km); C, continental-to-global (> 4000km)

‡‡Grain: F, fine; C, coarse

Appendix 2. Studies included in the present meta-analysis. (N = 112)

Reference	Surrogate§	PSRR	Vert/Invert*	Thermy¶	System‡	Extent†	Grain‡‡	R^2	n	Effect size	Lin. AIC_c	Quad. AIC_c
Aava 2001	NPP	US	V	H	T	C	C	0.385	208	0.7258	664.32	646.524
Abramsky & Rosenzweig 1984a	Rain	UM	V	H	T	R	F	0.393	13	0.7363	51.08	49.788
Abramsky & Rosenzweig 1984b	Annual plant cover	P	V	H	T	R	F	0.494	12	0.8729	44.584	47.989
Ambrose et al. 2009	NPP	P	I	P	M	R	F	0.222	47	0.5116	32.851	35.205
Andrews & O'Brien 2010	AET	DcP	V	H	A/T	C	C	0.602	655	1.035	6223.608	6114.458
Bailey et al. 2004	Summer NDVI	P	V	H	T	L	C	0.490	16	0.8673	72.809	75.665
Bellocq & Gómez-Insausti 2005	AET	AcP	V	H	T	R	C	0.754	191	1.3263	-464.86	-477.807
Blackburn & Gaston 1996	NPP	DcP	V	H	?	C	C	0.600	116	1.0317	24.499	13.464
Bonte et al. 2004	PCA axis (nutrients)	P	I	P	T	R	F	0.416	28	0.7667	214.785	217.35
Brown 1973	AnnRain	UM	V	H	T	R	F	0.593	18	1.0205	66.513	58.885
Brown & Davidson 1977	AnnRain	AcP	I	P	T	C	F	0.580	19	1	70.334	67.47

Reference	Surrogate[§]	PSRR	Vert/ Invert[*]	Thermy[¶]	System[‡]	Extent[†]	Grain[‡‡]	R^2	n	Effect size	Lin. AIC$_c$	Quad. AIC$_c$
Buckton & Ormerod 2002	NPP	DcP	V	H	A/T	C	C	0.463	82	0.8299	-8.476	-14.034
Carnicer et al. 2007	NDVI	P	V	H	T	R	C	0.249	310	0.548	2156.918	2158.728
Chase & Leibold 2002a	Algal biomass accrual	DcP	V/I	P	A	R	C	0.925	10	1.969	189.615	178.523
Chase & Leibold 2002b	Algal biomass accrual	UM	V/I	P	A	L	F	0.380	30	0.7192	66.218	61.396
Chase & Ryberg 2004a	Periphyon growth	UM	V/I	P	A	R	F	0.618	10	1.0612	62.293	59.436
Chase & Ryberg 2004b	Periphyon growth	UM	V/I	P	A	R	C	0.542	10	0.9421	64.218	62.589
Chiba 2007	DCA axis	UM	I	P	T	L	F	0.346	86	0.6749	428.998	395.35
Clarke & Scruton 1997	Biomass	P	I	P	A	R	F	0.282	20	0.5916	126.202	129.068
Cochrane et al. 2009	Water column productivity	P	I	P	M	R	F	0.216	47	0.5034	464.546	466.443
Costa et al. 2007	NPP	UM	V	P	T	R	C	0.048	201	0.2227	1827.66	1821.594
Cowlishaw & Hacker 1997a	Latitude	AcP	V	H	T	C	C	0.935	37	2.0432	160.693	80.252
Cowlishaw & Hacker 1997b	Latitude	AcP	V	H	T	C	C	0.933	35	2.0275	156.615	81.763

Reference	Surrogate[§]	PSRR	Vert/Invert[*]	Thermy[¶]	System[‡]	Extent[†]	Grain[‡‡]	R^2	n	Effect size	Lin. AIC$_c$	Quad. AIC$_c$
Currie 1991a	NPP	AcP	V	P	?	C	C	0.748	199	1.3124	2140.483	2014.238
Currie 1991b	NPP	US	V	P	?	C	C	0.347	208	0.6762	2742.278	2734.636
Davidson 1977	Rain	P	I	P	T	R	F	0.705	10	1.22	41.766	46.952
De los Rios & Soto 2007	Chl a	NS	I	P	A	R	C	0.172	14	0.4413	64.833	68.798
De Troch et al. 2006	Fraction Chl a/TOM	DcP	I	P	M	C	F	0.531	54	0.9259	260.715	258.886
Death & Winterbourn 1995	Phytopigment	DcP	I	P	A	L	F	0.544	55	0.9451	399.436	388.901
Death & Zimmerman 2005	Chl a	UM	I	P	A	L	F	0.366	70	0.701	377.309	367.754
Ding et al. 2005	NPP	DcP	V	H	T	L	C	0.701	50	1.2119	303.974	289.717
Dingle et al. 2000	Rainfall	P	I	P	T	R	C	0.515	33	0.9028	358.248	359.997
Dodson 1991	Photosynthetic flux	UM	I	P	A	C	C	0.266	22	0.5705	125.79	122.629
Dodson 1992	Phytoplankton production	DcP	I	P	A	C	C	0.389	44	0.731	-27.733	-31.495
Eggleton et al. 1994a	NPP	AcP	I	P	T	C	C	0.468	46	0.8368	442.479	438.197

Reference	Surrogate[§]	PSRR	Vert/Invert[*]	Thermy[¶]	System[‡]	Extent[†]	Grain[‡‡]	R^2	n	Effect size	Lin. AIC$_c$	Quad. AIC$_c$
Eggleton et al. 1994b	NPP	AcP	I	P	T	C	C	0.458	41	0.8231	331.814	328.899
Eggleton et al. 1994c	NPP	P	I	P	T	C	C	0.443	32	0.8028	228.58	229.477
Ellingsen & Gray 2002	Depth	UM	I	P	M	R	F	0.290	101	0.6021	942.975	910.597
Escaravage et al. 2009	NPP	N	I	P	M	R	F	0.750	15	1.317	197.888	197.189
Friberg et al. 2009	Temp	NS	I	P	A	L	F	0.014	10	0.1189	60.077	60.842
Fu et al. 2007a	AET	AcP	V	P	T	R	C		36	1.6668	263.792	262.806
Fu et al. 2007b	AET	P	I	P	T	R	C	0.762	33	1.3452	203.078	203.523
Gardezi & Gonzalez 2008	PET	AcP	V	P	A	R	C	0.058	7885	0.2457	-598.776	-626.613
González -Megias et al. 2008	Plant cover	P	I	P	T	L	F	0.383	10	0.7232	94.809	100.744
González-Taboada et al. 2009	NDVI	UM	V	H	T	R	C	0.127	194	0.3727	1353.093	1336.277
Gotelli & Ellison 2002	Latitude	P	I	P	T	R	C	0.315	22	0.6347	143.858	144.769
Hawkins & Porter 2003a	AET	AcP	I	P	T	C	C	0.819	162	1.4991	1477.675	1475.64

Reference	Surrogate[§]	PSRR	Vert/Invert[*]	Thermy[¶]	System[‡]	Extent[†]	Grain[‡‡]	R^2	n	Effect size	Lin. AIC$_c$	Quad. AIC$_c$
Henningson & Alerstam 2005	NPP	DcP	V	H	A/T	C	C	0.274	34	0.5811	187.675	186.558
Herzog & Kessler 2006	Canopy height	AcP	V	H	T	R	C	0.650	13	1.1162	116.514	115.055
Herzog et al. 2005	Elevation	P	V	H	T	L	C	0.768	12	1.3598	107.449	112.076
Hoffman & Dodson 2005	NPP	P	I	P	A	C	C	0.666	10	1.145	88.437	90.053
Hoyer & Canfield 1994	Integrated phosphorous	P	V	H	A	R	C	0.257	46	0.5586	326.25	327.749
Hurlbert & Haskell 2003	NDVI	P	V	H	T	C	C		832	1.0596	-1040.551	-1056.1
Jonsson et al. 2001	Coarse POM	NS	I	P	A	R	F	0.028	23	0.1689	104.363	106.063
Josefson & Hansen 2004	Biomass	NS	I	P	M	R	F	0.006	26	0.0776	260	262.813
Kaspari et al. 2000	NAP	P	I	P	T	C	F	0.903	15	1.8345	49.244	49.437
Kaspari et al. 2004	NPP	P	I	P	T	C	F	0.195	96	0.4742	374.306	375.893
Keil et al. 2008	AET	DcP	I	P	?	C	C	0.563	143	0.9737	1014.409	1010.649
Kerr & Currie 1999a	AET	P	I	P	A	C	C	0.749	251	1.3147	959.412	961.274

Reference	Surrogate[§]	PSRR	Vert/ Invert[*]	Thermy[¶]	System[‡]	Extent[†]	Grain[‡‡]	R^2	n	Effect size	Lin. AIC$_c$	Quad. AIC$_c$
Koh et al. 2006	NDVI	P	V	H	T	L	C	0.253	141	0.5533	-120.804	-119.778
MacDonald et al. 2010	Depth	DcP	I	P	M	R	F	0.562	24	0.9722	157.253	156.429
Moreno-Rueda & Pizzaro 2009	AnnRain	UM	V	H	T	R	C	0.099	5070	0.3257	47724.168	47365.77
Morton & Davidson 1988	AnnRain	NS	I	P	T	R	F	0.090	19	0.3095	86.684	89.897
Oberdorff et al. 1995	NPP	AcP	V	P	A	C	?	0.194	292	0.4728	300.681	296.854
Owen 1988a	NPP	DcP	V	H	T	R	C	0.338	189	0.6645	914.818	824.208
Owen 1988b	NPP	DcN	V	H	T	R	C	0.564	189	0.9752	886.756	851.773
Owen & Dixon 1989a	AnnRain (DCA Axis)	UM	V	P	?	R	?	0.374	139	0.7114	717.61	690.081
Owen & Dixon 1989b	AnnRain (DCA Axis)	N	V	P	T	R	C	0.263	148	0.5666	1217.513	1194.104
Owen & Dixon 1989c	AnnRain (DCA Axis)	US	V	P	?	R	C	0.327	54	0.6503	257.997	264.483
Owen & Dixon 1989d	AnnRain (DCA Axis)	NS	V	P	T	R	C	0.019	189	0.1387	1190.99	1193.069
Owen & Dixon 1989e	AnnRain (DCA Axis)	P	V	P	?	R	C	0.720	98	1.2509	430.005	431.529

Reference	Surrogate[§]	PSRR	Vert/ Invert[*]	Thermy[¶]	System[‡]	Extent[†]	Grain[‡‡]	R^2	n	Effect size	Lin. AIC_c	Quad. AIC_c
Pearson & Carroll 1998a (birds)	AnnRain	P	V	H	T	R	C	0.463	67	0.8299	629.16	630.169
Pearson & Carroll 1998b (butterflies)	AnnRain	AcP	I	P	T	R	C	0.699	67	1.2079	666.786	650.876
Pearson & Carroll 1998c (tiger beetles)	AnnRain	P	I	P	T	R	C	0.194	67	0.4728	423.094	424.65
Pérez-Mendoza et al. 2003	Depth	US	I	P	M	R	F	0.559	10	0.9676	75.671	75.671
Pouilly et al. 2006	Elevation	P	V	P	A	L	C	0.560	12	0.9692	78.979	82.013
Poulin et al. 2003	Host biovolume	P	I	P	A/T	C	C	0.218	131	0.5061	796.528	797.869
Powney et al. 2010	AET	US	V	P	T	C	C	0.146	751	0.4025	5838.608	5808.162
Qian et al. 2007a	NPP	P	V	P	T	C	C	0.675	205	1.1617	-42.886	-40.871
Qian et al. 2007b	NPP	AcP	V	P	T	C	C	0.564	202	0.9752	2.075	-4.286
Quiroga et al. 2009	Depth	UM	V/I	P	M	R	C	0.511	15	0.897	138.986	131.539
Renaud et al. 2006	Depth	P	I	P	M	R	F	0.327	16	0.6503	113.69	114.695

Reference	Surrogate[§]	PSRR	Vert/Invert[*]	Thermy[¶]	System[‡]	Extent[†]	Grain[‡‡]	R^2	n	Effect size	Lin. AIC_c	Quad. AIC_c
Rex 1981a	Depth	UM	I	P	M	?	?	0.706	16	1.222	87.206	75.301
Rex 1981b	Depth	UM	V	P	M	?	?	0.226	28	0.517	131.076	127.534
Rex 1981c	Depth	UM	I	P	M	?	?	0.601	25	1.0333	155.09	135.047
Rex 1981d	Depth	UM	I	P	M	?	?	0.246	63	0.544	323.851	312.944
Rex 1981e	Depth	UM	I	P	M	?	?	0.445	21	0.8055	117.098	111.332
Rex 1981f	Depth	NS	I	P	M	?	?	0.243	12	0.54	51.615	53.702
Rodríguez et al. 2005	AET	DcP	V	P	?	R	C	0.633	184	1.0865	-93.535	-88.022
Rosa et al. 2008	NPP	P	I	P	M	C	C	0.560	17	0.9692	144.112	146.526
Rowe 2009a	EVI	P	V	H	T	L	C	0.451	19	0.8136	110.569	112.496
Rowe 2009b	EVI	NS	V	H	T	L	C	0.044	16	0.2129	102.053	105.537
Rowe 2009c	EVI	US	V	H	T	L	C	0.549	16	0.9526	79.182	77.643
Rowe 2009d	EVI	NS	V	H	T	L	C	0.019	17	0.1387	102.295	104.47

Reference	Surrogate[§]	PSRR	Vert/ Invert[*]	Thermy[¶]	System[‡]	Extent[†]	Grain[‡‡]	R^2	n	Effect size	Lin. AIC_c	Quad. AIC_c
Ruggiero & Hawkins 2008	AET	AcP	V	H	T	C	C	0.721	1535	1.253	-1796.435	-1809.34
Sanders et al. 2007	NPP	N	I	P	T	L	C	0.276	22	0.5837	139.024	139.544
Schlacher et al. 2007	Depth	NS	I	P	M	R	F	0.194	14	0.4728	112.529	116.524
St-Lois et al. 2009	NDVI	DcP	V	H	T	L	C	0.633	42	1.0865	248.354	234.912
Storch et al. 2006	AET	DcP	V	H	?	C	C	0.546	16455	0.9481	195927.065	194677.9
Symonds & Johnson 2008	AET	DcP	V	P	T	R	C	0.302	67	0.6177	605.526	601.855
Tedesco et al. 2007	Rate of litter decomposition	DcP	V	P	A	L	C	0.720	14	1.2509	72.084	70.422
Tognelli & Kelt 2004	AET	P	V	H	T	C	C	0.659	1828	1.1323	14594.328	14627.18
Tsurim et al. 2009	Annual plant cover	DcP	V	H	T	L	C	0.435	23	0.792	102.763	96.312
Ulrich 2004	Biomass	P	I	P	T	L	F	0.861	92	1.6431	975.37	969.578
van Rensburg et al. 2002	NPP	P	V	H	T	R	C	0.516	101	0.7183	1124.207	1125.352
Verschuyl et al. 2008	NDVI	DcP	V	H	T	R	C	0.463	270	0.8299	1279.629	1270.088

Reference	Surrogate[§]	PSRR	Vert/Invert[*]	Thermy[¶]	System[‡]	Extent[†]	Grain[‡‡]	R^2	n	Effect size	Lin. AIC$_c$	Quad. AIC$_c$
Ward 1986	Biomass	DcP	I	P	A	L	?	0.572	11	0.9875	108.323	110.022
Whiteside & Harmsworth 1967	Phytoplankton Production	N	I	P	A	L	F	0.806	20	1.4606	34.544	35.564
Wollenburg & Kuhnt 2000	Carbon flux	UM	I	P	M	C	F	0.603	37	1.0366	306.789	281.966
Woodd-Walker et al. 2002	Latitude	DcP	I	P	M	C	C	0.656	171	1.1268	958.259	956.736
Wright 1983	NPP	P	V	H	A/T	C	C	0.265	28	0.5692	339.413	342.092
Zhao et al. 2006	AET	AcP	V	P	A	C	C	0.495	95	0.8743	87.831	87.048

*Vert/Invert: V, vertebrate; I, invertebrate; V/I, both

¶ Thermy: H, homeotherm; P, poikilotherm

‡System: T, terrestrial; A, freshwater aquatic; M, marine; A/T, freshwater aquatic & terrestrial

†Extent: L, local-to-landscape (0–200km); R, regional (200–4000km); C, continental-to-global (> 4000km)

‡‡Grain: F, fine; C, coarse

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