

Functional diversity within a morphologically conservative genus of predators: implications for functional equivalence and redundancy in ecological communities

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Summary

1. The idea that sets of species may have similar effects on population, community or ecosystem processes is a prevalent theme in many areas of ecology, especially in the context of biodiversity and ecosystem function. If indeed species are functionally equivalent, limiting similarity suggests that it should be closely related, morphologically similar species using similar resources in a similar manner.
2. We assayed the functional equivalence of three congeneric, morphologically similar predatory fish species (genus *Enneacanthus*). Functional equivalence was evaluated using aspects of both effects of fish on a variety of prey responses and the growth responses of the fish themselves as a measure of energy consumption. Fish were matched by initial size to control for effects of body size. A strict definition of functional equivalence based on niche theory was used to delineate it from the alternative of functional diversity.
3. Based on observed effects on larval anurans, only a single species pair could roughly be judged functionally equivalent, but these two species showed the greatest differences in growth rate and, hence, metabolic demand. Using the criterion of relative yield total, again, only a single pair could roughly be judged equivalent, however, members of this alternative species pair were dramatically different in their effects on larval anurans. Thus, as previously shown for a more diverse set of species, grouping of species by similarity in effects depends upon the specific response variable.
4. Overall range of effects produced on a variety of response variables was surprising, given the similarity in morphology and autecology, strong phylogenetic affinity, and the fact that neither predator size nor growth explained significant variation. Each species appears to be interacting with the environment in a different manner, either as a consequence of differences in metabolic demand or differences in preferences or efficiency with regard to prey types.
5. Observed responses are consistent with the predictions of niche theory and support an alternative explanation for observed relationships between diversity and ecosystem function. Our work suggests that functional equivalence may be uncommon, difficult to predict *a priori*, and that functional diversity, not functional equivalence, may underlie observed diversity–ecosystem function relationships.

Key-words: ecosystem function, functional redundancy, niche, species diversity, species turnover

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Introduction

Functional equivalence in community ecology encompasses the idea that species in natural communities are

similar in effects on population, community or ecosystem processes, and therefore play the same ‘ecological role’ (Lawton & Brown 1993; Kurzava & Morin 1998; Chalcraft & Resetarits 2003a,b; Loreau 2004), analogous to the concept that different structures may serve the same function in different organisms (*sensu* Alfaro, Bolnick & Wainwright 2005). Ecology has a long history

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of describing similar species, particularly those with allopatric ranges, as 'ecological equivalents,' suggesting the same functional role in their respective communities (e.g. Beauchamp & Ulllyott 1932; Elton & Miller 1954; Ross 1957; Pianka 1973; Bazzaz & Pickett 1980). This concept has been extended to species within communities and is now prevalent in both food web theory (e.g. Hairston, Smith & Slobodkin 1960; Fretwell 1977; Oksanen *et al.* 1981; McQueen, Post & Mills 1986; Menge & Sutherland 1987), and theory concerning the relationship between diversity and ecosystem function (Lawton & Brown 1993; Aarssen 1997; Huston 1997; Allison 1999; Petchey & Gaston 2002a, 2006; Loreau 2004). It also constitutes the fundamental assumption of neutral theory (Hubbell 2005, 2006).

The idea of functional equivalence is specifically embodied in the concept of 'functional groups;' (i.e. entities within which functional equivalence exists), (Lawton & Brown 1993; Stone, Dayan & Simberloff 2000; Chalcraft & Resetarits 2003a; Loreau 2004; Petchey & Gaston 2006). Functional groups are typically identified *a priori* based on similarity in morphology, life-history, and/or phylogeny (Schwartz *et al.* 2000; see Chalcraft & Resetarits 2003b for review) and used in the formulation of community assembly rules (Fox 1987; Fox & Brown 1995). Though community assembly rules based on functional groups remain controversial (e.g. Fox & Brown 1995; Wilson 1995; Stone, Dayan & Simberloff 1996; Brown, Fox & Kelt 2000; Stone *et al.* 2000), as does the dependence of ecosystem function on functional redundancy (Chalcraft & Resetarits 2003a,b; Loreau 2004; Petchey & Gaston 2006), the idea that such simple criteria as membership in a genus, functional group or guild can inform us about both community assembly and ecosystem function is very compelling (Stone *et al.* 2000).

But does functional equivalence exist within communities, and can we predict *a priori* which species are functionally equivalent and thus potentially interchangeable or compensatory in effect? Functional equivalence would suggest that ecologists can simplify systems by focusing on functional groups (i.e. sets of such functionally equivalent species) rather than individual species (Leibold & McPeck 2006). If functionally equivalent species co-occur within local communities; species can presumably be lost without significant negative effects on ecosystem function; if they co-occur at the regional level, regional loss of species can be compensated by expansion of such equivalent species (e.g. Fox 1987; Walker 1992; Naeem 1998; Yachi & Loreau 1999; Jaksi 2003; Loreau 2004). The majority of data brought to bear on functional redundancy is indirect, deriving from the observation that experimental reductions in species diversity can cause a nonlinear change in ecosystem function (Naeem *et al.* 1995; Naeem 1998; Wootton & Downing 2003). Moreover, citing as evidence of redundancy the fact that different species may have very similar effects on a few very broad measures of 'ecosystem function'

(Kurzava & Morin 1998; Chalcraft & Resetarits 2003a) ignores the vast complexity of ecological systems and the variety of so-called 'services' they provide. Communities that dramatically differ in species composition may have the same levels of community respiration, productivity or similar measures, but provide dramatically different levels of other important variables. For example, aquatic communities dominated by different taxa at a given trophic level (e.g. herbivorous tadpoles vs herbivorous zooplankton) may have similar total herbivore production (one measure of ecosystem function), but the rate at which energy is transported into terrestrial communities as spatial subsidies (another measure of ecosystem function) as a result of metamorphosis is totally different (tadpoles metamorphose into terrestrial adults whereas zooplankton do not have a terrestrial stage). Similarly, the extent of linkage between discrete aquatic communities and across the aquatic-terrestrial interface is markedly different if the herbivore trophic level is dominated by species with markedly different life-histories (Resetarits, Binckley & Chalcraft 2005).

Experiments have addressed whether specific species pairs are functionally equivalent, however, there are difficulties in using pairwise experiments conducted at different times, by different investigators, under different conditions, to gain a general understanding of the potential prevalence and distribution of functional equivalence (Chalcraft & Resetarits 2003a). Paine (1992) found that a variety of consumers were functionally equivalent largely as a consequence of being weak interactors, while Harris (1995) found general equivalence among a set of herbivores, but suggested that hers was not a fully adequate test. Our previous work identified little functional equivalence among predators that varied in higher level taxonomy, habitat and gape (Chalcraft & Resetarits 2003a,b). These studies dealt with morphologically and taxonomically diverse species that, nonetheless, could potentially be grouped under commonly used criteria (trophic level, guild, taxon, etc.).

The competitive exclusion principle and the concept of limiting similarity suggest that if equivalence exists, it is most likely among closely related, morphologically similar species that use similar resources in a similar manner (Fox 1987; Petchey & Gaston 2002a; Loreau 2004; Leibold & McPeck 2006). Functional groups, however, are typically identified *a priori* based on similarity in morphology, phylogeny or life-history using a rather broad brush approach (Schwartz *et al.* 2000; Chalcraft & Resetarits 2003b; Wright *et al.* 2006). For example, levels of morphological similarity used to assign species to functional groups are rarely based on empirical assessment of a species fundamental niche or its functional morphology in relation to potential niche axes. The basic question is; can we assume functional equivalence at any level in the absence of more detailed empirical assessment? The fundamental utility of the functional group concept is that one can lump organisms by means of readily identifiable traits

and then ignore differences below the level of the functional group; if we must empirically determine the makeup of functional groups, or if functional equivalence is rare, the utility is lost. Thus, experiments are needed that examine functional equivalence at the most basic level, within sets of taxonomically and morphologically similar species that would form the fundamental unit of any *a priori* classification of functional equivalence; '... our evolutionary considerations do suggest that ecologically similar species are more likely to be closely related to one another ...' (Leibold & McPeck 2006). Such species serve as a benchmark for examination of functional equivalence and its potential contribution to ecosystem function via functional redundancy.

We tested functional equivalence among three species that comprise the monophyletic centrarchid genus *Enneacanthus* (Sweeney 1972; Roe, Harris & Mayden 2002). Following earlier work (Harris 1995; Chalcraft & Resetarits 2003a; Loreau 2004), we take a strict view of functional equivalence; functional equivalence is the lack of a significant difference in performance between monospecific cultures of species under the same environmental conditions (Chalcraft & Resetarits 2003a,b, Loreau 2004), or *sensu* Harris (1995) 'in the absence of further information it would seem wise to avoid grouping together any species that are known to have statistically significant differences among their effects ...' Performance can be assayed in many ways, including growth and reproduction (e.g. relative yield totals; Loreau 2004), and suppression of a given resource(s) (e.g. Chalcraft & Resetarits 2003a,b). Any less rigorous definition confuses functional equivalence with functional diversity, which is an equally viable mechanism for the provision of ecological 'insurance' (Petchey & Gaston 2002a,b, Chalcraft & Resetarits 2003a,b; Loreau 2004; Petchey & Gaston 2006). In this context, functional equivalence supports ecosystem function via functional redundancy, whereas functional diversity supports ecosystem function via functional complementarity (Kurzava & Morin 1998). We discuss the importance of the distinction and the implications for ecological and evolutionary theory below. In the present study, functional equivalence was not a feature of members of the genus *Enneacanthus* despite the similarity in morphology, life-history and phylogeny that would typically place them in the same functional group.

Materials and methods

Enneacanthus is a distinctive genus of dwarf sunfish (Centrarchidae) confined primarily to the Atlantic slope of the eastern USA (Sweeney 1972). *Enneacanthus chaetodon* (Baird), *E. gloriosus* (Holbrook) and *E. obesus* (Girard) (Fig. 1), are broadly sympatric in a variety of habitats (e.g. small ponds, river swamps, reservoirs). *Enneacanthus gloriosus* is the most common and uniformly distributed, while *E. chaetodon* and *E. obesus* are typically found in more acidic, oligotrophic

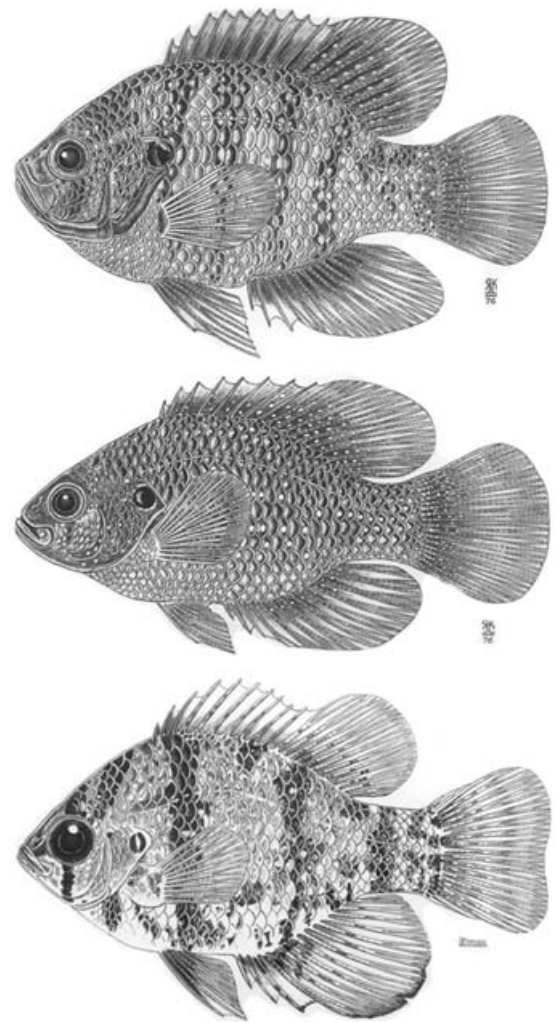


Fig. 1. *Enneacanthus obesus* (top), *E. gloriosus* (middle), *E. chaetodon* (bottom), illustrating morphological similarity. Drawings by R. Kuhler used with permission of the North Carolina State Museum. Reproduced with permission from Lee *et al.*, 1980. *Atlas of North American Freshwater Fishes*. N.C. State Museum of Natural Sciences.

habitats (Sweeney 1972; Gonzalez & Dunson 1989, 1991). All pairs may be syntopic, but very rarely all three. *Enneacanthus gloriosus* is the largest (adult size: 61–78 mm SL), followed by *E. obesus* (51–70 mm SL) and *E. chaetodon* (29–66 mm SL). All three are morphologically conservative, generalist predators on small invertebrates and vertebrates. These species would clearly meet the *a priori* criteria for inclusion in the same functional group for most adherents, but detailed studies of functional morphology and autecology for these, as well as most other species, could likely identify differences sufficient to support differences in function (e.g. Graham 1986). Nonetheless, broad distributional overlap, similarity in morphology and autecology, and importance in small lentic habitats in the Atlantic drainage (e.g. Resetarits & Wilbur 1989; Bristow 1991; Binckley & Resetarits 2003; Chalcraft & Resetarits 2003a,b, 2004) make the genus an excellent candidate for testing functional equivalence.

We evaluated how a three-species ensemble of larval anurans responded to variation in predator identity in replicated artificial ponds. Our experiment consisted of four treatments, three species of *Enneacanthus* and a predator-free control, each replicated four times in a randomized complete block design. We created a hexagonal array of 16 artificial ponds (1100 L cattle tanks) in a clearing at Naval Security Group Activity Northwest (NSGANW) in SE Virginia, identifying four spatial clusters of four ponds each as statistical blocks. We conducted all procedures (e.g. creation, manipulation and monitoring of ponds) by block to minimize variation within blocks not attributable to treatment.

We filled tanks on 5–6 April 2001 to 50 cm (volume: c. 1000 L) with water from a nearby borrow-pit. A 2 mm mesh filter placed over the pump intake prevented uptake of larval anurans or their predators. Zooplankton, periphyton and phytoplankton could pass through the filter and served as alternative prey for predators and food for larval anurans. Immediately after filling, we covered tanks with tight-fitting fibreglass window screening to prevent unwanted colonization by predatory insects and ovipositing treefrogs, and to retain experimental organisms. On 7 April 2001 we added to each tank 1 kg of forest leaf litter for structural complexity and nutrients, and a supplemental 500-mL mixture of zooplankton, periphyton, phytoplankton and macroinvertebrates from ponds and ditches at NSGANW (potential predators were removed).

Each tank received 300 newly hatched tadpoles each of *Bufo terrestris* (Bonnaterre), *Rana sphenocephala* (Cope) and *Hyla squirella* (Bosc) on 11 June 2001 (initial density of 900 individuals/pond). Tadpoles represented 12 clutches of *Bufo*, 8 of *Rana* and 37 of *Hyla*, differences reflecting clutch size. Each pond received a similar fraction from each clutch to ensure similar genetic diversity among ponds within species. Next day we randomly assigned treatments to ponds within each block with predator treatments each receiving one fish. We matched size ranges for our juvenile fish, ranked them by size within species, and assigned individuals of the same rank size to blocks [initial mass (mean \pm 1 SE): 2.828 \pm 0.279 g (*E. chaetodon*), 2.910 \pm 0.327 g (*E. gloriosus*), 2.750 \pm 0.272 g (*E. obesus*)]. Initial densities fell within the range observed for adults in natural ponds (Bristow 1991; Chalcraft & Resetarits, personal observation). Using identical densities and matched body sizes allows evaluation of per capita effects independent of differences in density and size.

We monitored the ponds daily, collected anurans as they initiated metamorphosis (emergence of at least one forelimb), and weighed metamorphs (wet mass) upon tail resorption. Between 24 and 25 September 2001 (total duration 105–106 days) we drained all ponds and counted and weighed survivors, producing a complete census of survivors. Most *Bufo* had completed metamorphosis, while only a single *Rana* had metamorphosed. No *Hyla* survived in any tanks.

DATA ANALYSIS

We quantified predator effects on individual species responses (survival and mass for *Rana* tadpoles; survival, metamorph mass and proportion metamorphs for *Bufo*) and larval ensemble responses (number and total biomass of anurans and final proportional abundance of *Bufo*). Proportion metamorphs is a surrogate for development rate, measuring the fraction of the population passing a particular developmental stage (metamorphosis). Total number and biomass measure importance of larval anurans to pond food webs; food web models suggest ensembles with greater biomass or number have greater impacts on food resources (Hairston *et al.* 1960; Fretwell 1977; Oksanen *et al.* 1981; McQueen *et al.* 1986; Menge & Sutherland 1987). Analysis of final proportional abundances detected changes in composition independent of changes in total number (Morin 1983; Chalcraft & Resetarits 2003a). Proportional abundance of *Hyla* was not included as it was invariant (0%), thus, proportional abundance was solely dependent on the final proportional abundance of either remaining species (we chose *Bufo*). Survival was angularly transformed (arcsine squareroot), proportion metamorphs squareroot transformed (the latter because values were uniformly high), and both measures of anuran importance were \log_{10} transformed. Three separate MANOVAS were used to examine the effects on: (i) *Rana* responses; (ii) *Bufo* responses; and (iii) larval ensemble responses. We also analyzed mean total biomass of *Bufo* metamorphs as a measure of energy export to the terrestrial environment using ANOVA.

Use of several MANOVAS on logical data subsets is preferable to a single MANOVA with all response variables, as a large number of variables dramatically reduce the power. Furthermore, interpretation of MANOVAS conducted on subsets are more straightforward as response vectors describe a single effect of interest (Chalcraft & Resetarits 2003a). We also conducted univariate ANOVAS on each component (e.g. mass and survival) of the response vector, and pairwise comparisons of means following only significant ANOVAS using Fisher's LSD. Such protected comparisons using LSD reduce experimentwise Type I errors while also minimizing the occurrence of Type II errors (Carmer & Swanson 1973; Bernhardson 1975; Carmer & Walker 1982), and are more consistent in detecting specific treatment differences than other methods (Saville 1990, 2003). Block explained almost no variation for any response variable (exclusion/inclusion did not affect test outcomes), so block was rolled into the error term for simplicity of presentation.

Results

Survival was 100% for all *Enneacanthus* species and all individuals grew substantially (mean mass in grams [mean % change] \pm 1 SE: *E. chaetodon* 5.73 [203%] \pm

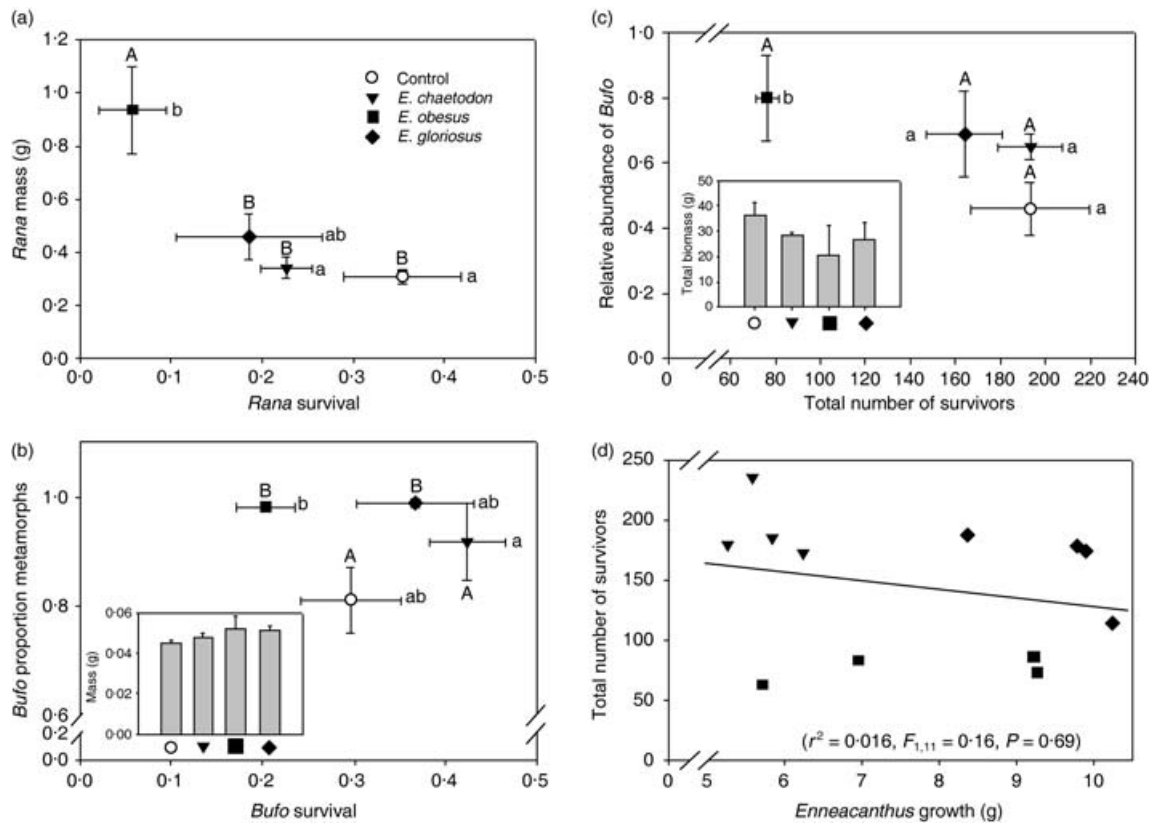


Fig. 2. (a) Mean \pm 1 SE for survival and mass of *Rana*, (b) mean \pm 1 SE for survival, proportion metamorphs and mass (inset – no significant differences), (c) mean \pm 1 SE for total number of survivors, relative abundance of *Bufo*, and total biomass (inset – no significant differences). Treatments sharing the same letter/case are not significantly different; capital letters represent the variable on the y-axis, lower case the variable on the x-axis, (d) relationship between individual predator growth and total number of survivors, illustrating lack of size/growth effects both among and within species. Legend same as in (a–c). Inset graphs in (b, c) represent variables with non-significant ANOVAs, thus, multiple comparisons among the means were not performed.

0.21, *E. gloriosus* 9.58 [329%] \pm 0.42; *E. obesus* 7.79 [283%] \pm 0.88), attaining adult body size by termination of the experiment. Growth differed significantly among species ($F_{2,8} = 9.99$, $P = 0.01$), but initial size did not significantly affect growth ($F_{1,8} = 0.05$, $P = 0.83$). Multiple comparisons revealed that *E. chaetodon* growth was significantly different from that of *E. gloriosus* and *E. obesus*, but the latter two were not significantly different.

Treatment had a highly significant effect on *Rana* survival and mass (MANOVA, Wilk's $\lambda = 0.2507$, $F_{6,22} = 3.66$, $P = 0.0114$; survival $F_{3,12} = 5.53$, $P = 0.0128$; mean tadpole mass $F_{3,12} = 8.66$, $P = 0.0025$) (Fig. 2a). The *E. obesus* treatment had significantly lower survival of *Rana* than *E. chaetodon* and Control tanks, while the *E. gloriosus* treatment did not differ significantly from other treatments (Fig. 2a). *Rana* with *E. obesus* were significantly larger than with other predators or in Controls (Fig. 2a).

Treatment had a significant effect on *Bufo* survival and proportion metamorphs but not on mass at metamorphosis (MANOVA Wilk's $\lambda = 0.2224$, $F_{9,24.5} = 2.33$, $P = 0.0471$; survival $F_{3,12} = 3.54$, $P = 0.0483$; proportion metamorphs $F_{3,12} = 4.95$, $P = 0.0183$; mass $F_{3,12} = 0.88$, $P = 0.4778$) (Fig. 2b). *Bufo* with *E. obesus*

had significantly lower survival than with *E. chaetodon*; Control and *E. gloriosus* tanks were intermediate and not significantly different from the other treatments (Fig. 2b). A greater proportion of *Bufo* metamorphosed in *E. obesus* and *E. gloriosus* treatments than in Control and *E. chaetodon* treatments (Fig. 2b); there was no significant difference in *Bufo* mean mass at metamorphosis among treatments (Fig. 2b inset).

From a whole ensemble perspective, MANOVA revealed highly significant variation among treatments in the multivariate vector of total biomass, total number of survivors, and relative abundance of *Bufo* (Wilk's $\lambda = 0.1359$, $F_{9,24.488} = 3.45$, $P = 0.007$). In univariate ANOVAs only total number was significant ($F_{3,12} = 17.92$, $P < 0.0001$, total biomass $F_{3,12} = 1.92$, $P = 0.18$, relative abundance $F_{3,12} = 2.22$, $P = 0.1389$) (Fig. 2c). Multiple comparisons revealed that the difference in total number was driven by the *E. obesus* treatment.

There was also significant variation among treatments in the extent of the spatial subsidies from the aquatic to the terrestrial environment, as measured by the total biomass of *Bufo* metamorphs (univariate ANOVA, $F_{3,12} = 3.75$, $P = 0.041$). In multiple comparisons, the *E. obesus* treatment was significantly different from both the *E. chaetodon* and *E. gloriosus* treatments,

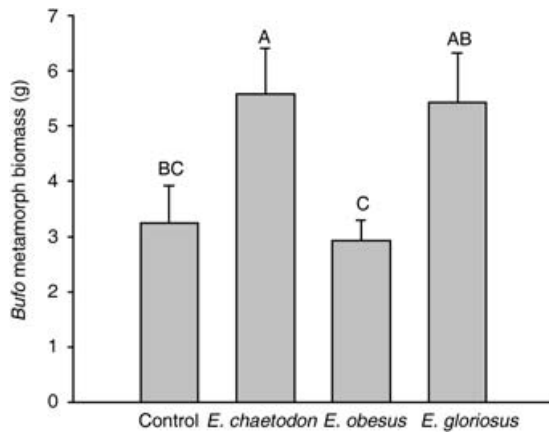


Fig. 3. Variation in energy transfer from the aquatic to the terrestrial environment as illustrated by the production of *Bufo* metamorphs in the four treatments (mean \pm 1 SE). Shared letters indicate means that are not significantly different. The *E. obesus* treatment produces significantly lower subsidies to the terrestrial environment than either *E. chaetodon* or *E. gloriosus*.

but not from the controls, while the Control and *E. chaetodon* treatments were also significantly different (Fig. 3).

Interestingly, very little variation in any response variable was explained by initial mass of predators or predator growth (change in mass) (all $r^2 < 0.09$ and all $P > 0.35$; e.g. Fig. 2d), which partly explains the lack of a block effect. Indeed, the rank order of effect size, which was consistent across all response variables (Fig. 2) (*E. obesus* > *E. gloriosus* > *E. chaetodon*) did not mirror either mean initial mass (see Materials and methods: *E. gloriosus* > *E. chaetodon* > *E. obesus*), which varied little among species, or growth (*E. gloriosus* > *E. obesus* > *E. chaetodon*), which varied considerably among species, as well as within *E. obesus* (Fig. 2d).

Discussion

FUNCTIONAL EQUIVALENCE IN *ENNEACANTHUS*

We previously demonstrated that functional equivalence is not characteristic of diverse sets of predators often designated as functional groups (Chalcraft & Resetarits 2003a), and that species sharing broadly similar traits (e.g. taxonomic affinities, gape size or microhabitat use) are not necessarily more similar in their functional effects (Chalcraft & Resetarits 2003b). The present study strengthens those conclusions by demonstrating that, even within a small, morphologically conservative genus of predators, functional equivalence is less likely than functional diversity. Of three species pairs, only one exhibits similarity remotely concordant with functional equivalence using the criterion of effect on specific resources (larval anurans) (Chalcraft & Resetarits 2003a,b). Using similarity of yield criterion (Loreau 2004) (similarity in ability to

extract energy from a community under similar conditions – similar to ‘importance’ in food webs), again only one pair could be judged functionally equivalent. Yet, it is a different species pair and equivalence is tenuous because of substantive differences in growth rate variation among individuals of the two species.

Enneacanthus obesus is distinct from both *E. gloriosus* and *E. chaetodon* in effects on almost all variables examined, except growth, where it is closer to *E. gloriosus* but shows considerable individual variation (Fig. 2d). Taxonomic and morphological similarities do not ensure similarity of effects; in the case of *E. obesus*, not even within a species. Differences in effects among species occurred despite no differences in initial size, and size and growth rate explained virtually no variation in effects on larval anurans. Further, similarity of effects could not be predicted based on similarity in morphology, as *E. obesus* is no less similar to *E. chaetodon* than is *E. gloriosus* (Sweeney 1972; Fig. 1), while molecular evidence indicates *E. gloriosus* and *E. obesus* are more closely related (Roe *et al.* 2002).

Figure 2d suggests an explanation for differences in effect. Given similarity of morphology and physiology, differences in growth (i.e. final body size) (sans reproduction) should indicate differences in metabolic demand and functional non-equivalence (Chalcraft & Resetarits 2004; Loreau 2004). *Enneacanthus chaetodon* exhibited relatively low growth and small effects on target prey. In contrast, *E. gloriosus* exhibited the highest growth (> 60% higher than *E. chaetodon*), but had similar effects on tadpole prey. Lastly, *E. obesus* displayed variable growth rates, overlapping with both *E. chaetodon* and *E. gloriosus*, but had uniformly strong effects on tadpoles. *Enneacanthus chaetodon*, as the smallest member of the genus, likely had small effects on target prey because of relatively small metabolic demand tied to limited growth potential. Similar effects of *E. gloriosus*, despite high growth rate, suggest that *E. gloriosus* focused on alternative invertebrate prey. Strong effects of *E. obesus*, irrespective of individual growth rate and metabolic demand, suggest they are effective predators on tadpoles and may prefer them over the available invertebrate prey. Each species does something sufficiently different to generate different effects on prey assemblages. This is precisely what niche theory would predict (Vandermeer 1972, Chase & Leibold 2003; Loreau 2004).

Even if productivity, community respiration or other metrics of ecosystem function remain the same within our aquatic habitats because of relative similarity in total anuran biomass, larval anurans are temporary residents of aquatic systems. Significant variation in the output of metamorphs based on predator identity (Fig. 3) signals variation in export of energy to surrounding terrestrial systems (spatial subsidies) and variation in connectivity between aquatic and terrestrial systems, as well as between discrete aquatic communities. These shifts in energy flow and connectivity with different predators further suggest that a single metric or limited

set of metrics may lead to misleading and oversimplified results.

What does it mean from the perspective of community function if only one of three species pairs is functionally equivalent, at least with respect to larval anurans? Or with respect to overall energy demand or export? At the local or regional level, only one pair may be substitutable with respect to any specific response variable. If *E. gloriosus* and *E. chaetodon* coexist in a given community and one is lost, the overall structure and function of the community may be preserved from the perspective of larval anurans (Loreau 2004), but not necessarily for zooplankton. However, if either of the other two species pairs coexist and one is lost, the basic structure and function of the community will necessarily change. On a regional scale, if we assume one species of *Enneacanthus* per community (largely the case in nature), replacement of one species by another in no way assures preservation of existing community structure and function. Interestingly, *E. gloriosus* and *E. obesus* are broadly sympatric, while *E. chaetodon* has a more restricted and sporadic distribution. When all three are sympatric, *E. obesus* and *E. chaetodon* are more likely syntopic (Lee & Gilbert 1980). Thus, across their distribution, co-occurring pairs are more likely complementary than equivalent in effects on community structure. Again, given the basic tenets of niche theory (Vandermeer 1972; Chase & Leibold 2003; Loreau 2004), this is hardly surprising.

Despite work dispelling the assumption that frequency and intensity of competition are always best predicted by morphological similarity (e.g. Brown & Davidson 1977; Polis & McCormick 1986; Morin, Lawler & Johnson 1988; Resetarits 1995a,b), limiting similarity remains a reasonable starting point for examining functional equivalence, because for similar species both effects on a community and ecological tolerances should be reasonably concordant (Wellnitz & Poff 2001). Our data illustrate the difficulty of predicting functional equivalence *a priori*, as morphologically and taxonomically similar species are not necessarily equivalent (Harris 1995; Chalcraft & Resetarits 2003a,b; Wright *et al.* 2006). Morphological similarity, similar phylogeny, guild membership, and even the combination of the three seen in *Enneacanthus* do not equate to functional equivalence. This leads us back to consideration of the species itself as the fundamental unit for defining functional roles.

PROSPECTS FOR FUNCTIONAL EQUIVALENCE WITHIN AND AMONG COMMUNITIES

Recent work suggests that, in terms of both the effects on ecological communities (functional roles) and responses to environmental variation (ecological responses), species identity is critical. Spatial and temporal turnover in species is associated with changes in the dynamics and functioning of the communities, metacommunities and ecosystems they comprise

(Leibold, *et al.* 1997; Chase & Leibold 2002, Chalcraft & Resetarits 2003a,b; Chalcraft *et al.* 2004; Resetarits 2005). What does this mean for the idea of functional equivalence? We suggest, based on our work on predators and on fundamental principles of niche theory, that functional equivalence should be rare within communities and that the mechanisms underlying diversity–function relationships derive most commonly from the diversity of ecological roles and the complex interactions within species rich communities (Petchey & Gaston 2002b; Chalcraft & Resetarits 2003a; Loreau 2004; Petchey & Gaston 2006), rather than from the provision of insurance specifically in the form of equivalence and redundancy (e.g. Elton 1958; Walker 1992; Naeem 1998; Yachi & Loreau 1999; Hubbell 2005, 2006).

Functional equivalence within communities necessarily implies that communities do not meet the equilibrium requirements for competitive exclusion (Gause 1934; Hardin 1960). Functional diversity implies that differences among species within communities exceed the ‘limiting similarity’ compatible with equilibrium coexistence (Hutchinson 1959; MacArthur & Levins 1967; Abrams 1983). We have known since Gause (1934) that asymmetry in the competition coefficients is necessary for competitive exclusion, thus, it has always been an option that species must either sufficiently differ in niche requirements, or must be sufficiently similar in both niche requirements and competitive abilities, in order to coexist (Aarssen 1983; Ågren & Fagerström 1984). Despite the possibility of coexistence by similarity, widespread functional equivalence within communities remains largely antithetical to ecological and evolutionary theory beginning with Darwin (Darwin 1859; Hutchinson 1959; Vandermeer 1972; Chase & Leibold 2003; Loreau 2004; Leibold & McPeck 2006). While neutral theory itself and recent considerations of the potential relationship between niche and neutral processes have reinforced the idea of the evolution of ecological equivalence and its persistence in at the local scale within communities, none of these considerations (with the obvious exception of strict neutral theory; Hubbell 2005, 2006) suggest that co-occurring sets of functionally equivalent species are the norm within ecological communities (Leibold & McPeck 2006; Scheffer & van Ness 2006). Plausible scenarios can be constructed that support local coexistence of ecologically equivalent species, but niche processes are still considered the dominant force in determining patterns of species coexistence (Aarssen 1983; Ågren & Fagerström 1984; Leibold & McPeck 2006; Scheffer & van Ness 2006).

While niche theory and the importance of competition have both fallen into and out of favour over the years, the general ideas remain central to our view of how ecological communities are assembled, as does the role of individual selection. And these concepts are largely incompatible with the idea of functional equivalence (Loreau 2004). Functional groups do not

evolve; that is, the purview of populations and species. Scheffer & van Ness (2006) have demonstrated that clusters consisting of essentially equivalent species can evolve and persist in theoretical communities, yet this occurs only in 'saturated' communities, and again is not expected to be the norm. This reinforces the idea that functional redundancy should not hold primacy as the mechanism driving relationships between biodiversity and ecosystem function. Thus, although functional equivalence among species in ecosystems experiencing diversity loss might be beneficial to ecosystem function, the ecological and evolutionary impetus for species to remain or become more similar in their resource use in sympatry remains problematic. The idea of character convergence, while not as old as that of character displacement, has a considerable history (MacArthur & Levins 1967; Cody 1973). Yet, it has always been postulated as the exception rather than the rule in ecological communities (MacArthur & Levins 1967; Cody 1973; Slatkin 1980; Scheffer & van Ness 2006). Even its most ardent supporters never suggested that ecological communities are dominated by convergence of competitors. And while the Clementsian ideas of community selection and community evolution have recently threatened to re-emerge (Morin 2003; Wilson & Swenson 2003), conceivably providing a 'mechanistic' framework for functional equivalence, until we reconcile such notions with individual selection and evolution we should be cautious in claiming that effects of diversity on ecosystem function derive from functional equivalence and functional redundancy. This is especially true when an equally viable explanation for ecological insurance, functional diversity, is supported by a vast corpus of ecological and evolutionary theory that suggests equivalence should be rare within communities and when present, selection should most often work to reduce such equivalence (Fig. 4).

Lost in the discussion of functional equivalence are differences in expectation between species functioning in a redundant capacity at the local scale (within communities) and those redundant at the regional scale (among communities – within metacommunities). Niche theory tells us expectations for redundancy at these two scales are not necessarily equivalent, because limiting similarity and competitive exclusion play a major role in restricting coexistence at the local scale (Fig. 5), but may enhance coexistence at the regional scale (Loreau & Mouquet 1999; Amarasekare & Nisbet 2001; Mouquet & Loreau 2002). Under equilibrium conditions, local redundancy is constrained by limiting similarity and competitive exclusion. If non-equilibrium mechanisms drive the local coexistence of similar competitors, the consequences for local redundancy are modified or constrained by the dynamics of more complex interactions among multiple species (i.e. keystone predators) or the continuing effects of abiotic factors such as disturbance. Maintenance of redundancy is then dependent upon other species/processes

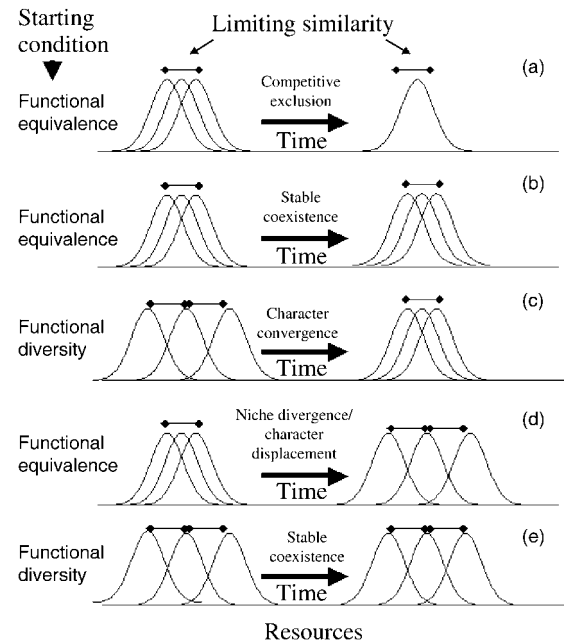


Fig. 4. Projections of species functional roles within communities through time on the basis of niche theory. Functional equivalence implies that differences among species within a functional group are less than the minimum level of similarity compatible with equilibrium coexistence (limiting similarity). In contrast, functional diversity implies that the differences are \geq the minimum level of similarity compatible with equilibrium coexistence, specifically the conditions expected in diverse, multi-species communities. The likelihood of finding functionally equivalent species in a community is dependent on: (i) the frequency with which particular ecological processes occur; (ii) the presence of functionally equivalent species in the regional species pool; and (iii) the co-occurrence of these functionally equivalent species within the community in the past or the evolution of functional similarity *in situ*. A large body of existing theory and data suggest that very similar species are unlikely to coexist in communities due to competitive exclusion (a). There is limited evidence suggesting that functional equivalence may persist in communities if the intensity of competitive interactions are very strong (b) or if character convergence occurs (c). However, on the basis of niche theory and a considerable body of empirical work, the more likely scenarios are that competition among functionally equivalent species forces niche divergence or character displacement (which promotes functional diversity, (d) or that the species present in the community were never functionally equivalent and their coexistence derives from functional diversity (e). Consequently, the three most likely scenarios (a,d,e) support the idea of functional diversity within communities, while the remaining two scenarios (b,c) that support functional equivalence have not been frequently documented, nor are strongly supported by theory (see text for additional discussion).

and is no longer a simple property of functional groups. Operationally, predicting functional equivalence at the local scale is highly problematic because predicting the limiting similarity and thus the optimum similarity for coexistence and functional equivalence is not straightforward, and is likely an empirical question (Fig. 5).

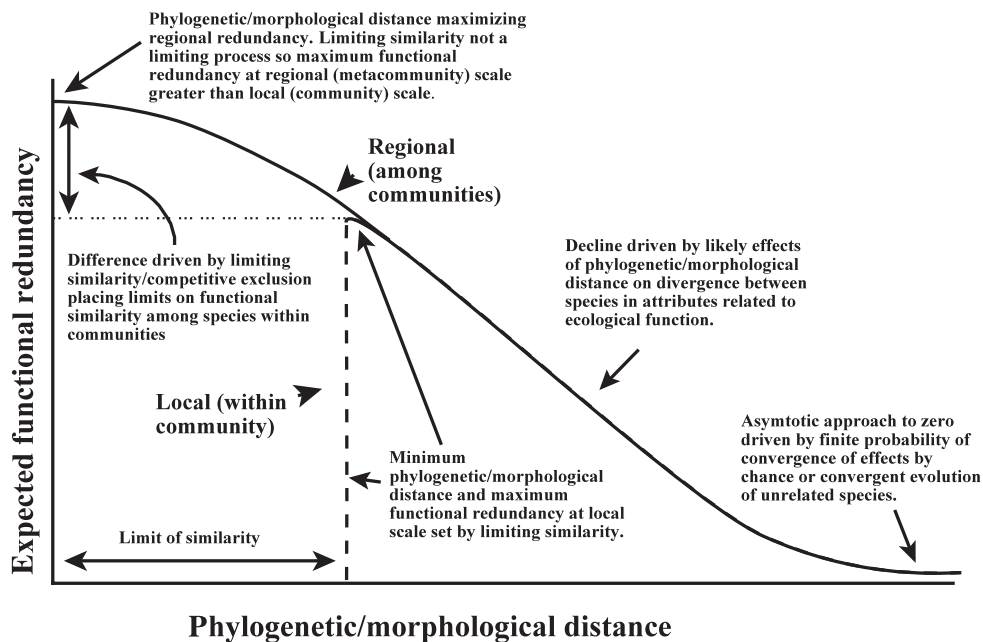


Fig. 5. Graphical model of the expected relationship between functional redundancy and phylogenetic/morphological similarity at the local (community; dash curve) and regional (metacommunity; solid curve) scales based on niche theory (see text). High β diversity allows functional redundancy to be higher at the regional scale than at the local scale. Although limiting similarity prevents redundant species from co-occurring at the local scale under equilibrium conditions (except in cases of near identity – see text), processes that generate spatial variation in species composition could allow functionally redundant species to co-occur at the regional scale. If there is little or no species turnover, the maximal level of redundancy at the regional scale is equal to that at the local scale.

Similarly, the idea that entire communities are assembled based primarily on species similarity, rather than species dissimilarity and the resultant sorting among a more diverse set of ecological roles, has little empirical or theoretical support; ‘Consequently, it seems unlikely that entire assemblages of species will evolve to be equivalent, even though subsets of species may’ (Leibold & McPeck 2006). Leibold (1998) suggest that species similarities within ensembles result from general similarities in species responses to the environment: Chesson’s (2000) ‘equalizing effects’ (e.g. Emberton 1995), whereas species differences result from or reflect species impacts on resources (which defines functional roles in our study; Chesson’s ‘stabilizing effects’ (2000)).

Vandermeer *et al.* (2002) recently suggested increased levels of competition may promote species coexistence under certain conditions. While application of this idea (as well as previous ideas on coexistence through similarity) to functional equivalence lends support, it also points to a second major flaw. If similar species pack into communities based on similar responses to the environment, or based on increased resource overlap and intensity of competition, then environmental change causing species loss should do so not via uniform loss across functional groups, but by eliminating similar sets of species, that is, members of a functional group or entire functional groups. Species more similar in effects on ecological communities are

also likely to be more similar in responses to environmental change (Wellnitz & Poff 2001). Thus, extinction probabilities should be correlated among members of a functional group, discounting the value of functional redundancy for providing ecological insurance. This is especially true if they share a common phylogenetic history. Counteracting this, of course, is co-occurring species with similar requirements diverging in resource use, which is again what niche theory would predict. Such divergence in resource use should, however, generate divergence in functional roles or, under Vandermeer *et al.*’s (2002) scenario, a reduction in competition and loss of species richness. Neither of these processes is compatible with functional equivalence underwriting ecological insurance. The broader concept of functional groups used to examine patterns of community assembly remains a potentially valid construct (see Fox 1987; Fox & Brown 1995; Wilson 1995; Stone *et al.* 1996; Brown *et al.* 2000; Stone *et al.* 2000), but whether functional groups, rather than niches themselves, form the basis of community assembly processes is an unresolved question.

Any attempts to simplify ecological systems have a cost in lost information. Our recent work and that of others suggests that when we simplify the world by ignoring species, that cost is often too great (Leibold *et al.* 1997; Chalcraft & Reseraris 2003a,b; Loreau 2004). While sets of species may have equivalent effects on natural communities, identification of those species

and assessment of their ability to coexist in ecological communities remain empirical questions. If, as Petchey & Gaston (2006) suggest, 'For functional classifications ... the correct number of traits is the number that are functionally important', the quantification of functional diversity (or functional equivalence) within communities is a major endeavour in and of itself, comparable in methodology and scope to phylogenetics or population genetics. This endeavour is justified in terms of its potential importance in understanding ecosystem function, community structure, and the evolution of diversity within communities, but simultaneously obviates the idea that simplistic notions of functional groups and ecological insurance based on functional redundancy allow us to ignore, without such detailed understanding, the basic differences in form and function implied by the classification of organisms into species. Patterns may exist in the distribution of functional equivalence among species, however, no simple *a priori* criterion is likely to provide a 'breakthrough' (*sensu* Stone *et al.* 2000) in simplifying communities and applying assembly rules (Fox 1987; Fox & Brown 1995). This clearly has consequences for how we continue to approach the study of ecological communities.

We have demonstrated that even morphologically similar congeners of the same initial size are not characterized by functional equivalence. Combined with recent theoretical (Loreau 2004) and empirical (Chalcraft & Resetarits 2003a,b) evidence, this suggests that functional equivalence is likely rare, at least at higher trophic levels, and supports the accompanying proposition that the positive effects of species diversity on ecosystem function derives, rather, from functional diversity. This should not disillusion ecologists in the search for pattern and generality. On the contrary, this proposition derives directly and logically from 150 years of ecological and evolutionary theory and accompanying empirical research. Rather, it is the prospect that functional equivalence is the norm within communities that should shake us to our foundational roots and force us back to the drawing board of ecological theory.

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