

Taxonomic relatedness does not matter for species surrogacy in the assessment of community responses to environmental drivers

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Summary

1. Taxonomic sufficiency concerns the use of higher-taxon diversity as a surrogate for species diversity. It represents a fast and cost-effective method to assess community responses to natural and anthropogenic environmental drivers. In spite of the potential applications of using higher taxa as surrogates for species, little research has been carried out to determine the underlying reasons that might make taxonomic surrogacy effective for detecting diversity changes.

2. Here, we determine whether the effectiveness of higher taxa as species surrogates relies mostly on taxonomic relatedness of species (i.e. the relative closeness of species in the Linnaean taxonomic hierarchy) or depends simply on the numerical ratio between species and higher taxa (i.e. the degree of species aggregation). We reviewed the current literature on taxonomic sufficiency to check for any correlation between the effectiveness of higher taxa and the degree of species aggregation across different types of organisms. Tests based on random simulations from diverse marine mollusc assemblages were also carried out to ascertain whether the ability of higher taxa to detect variation in the multivariate structure of assemblages depended on the degree of species aggregation.

3. Mollusc data showed that information loss and the ensuing decrease in statistical power to detect natural or human-driven changes in assemblages at higher taxonomic levels depend on the degree of species aggregation, rather than on the taxonomic resolution employed. Analyses of the literature suggested that such outcomes could be generalizable to a wide range of organisms and environmental settings.

4. Our findings do not support the idea of a direct relationship between taxonomic relatedness and ecological similarity among species. This indicates that taxonomic ranks higher than species may not provide ecologically meaningful information, because higher taxa can behave as random groups of species unlikely to convey consistent responses to natural or human-driven environmental changes.

5. *Synthesis and applications.* Surrogates of species-level information can be based on the 'highest practicable aggregation' of species, irrespective of their taxonomic relatedness. Our findings cast doubt on static taxonomical groupings, legitimizing the use of alternative ways to aggregate species to maximize the use of species surrogacy.

Key-words: biodiversity, conservation, higher-taxon approach, impact assessment, marine molluscs, natural environmental variations, phylogenetic relatedness, taxonomic surrogates, taxonomy

Introduction

There is an urgent need to find ways of coping with escalating human threats to ecosystems worldwide (Sanderson *et al.*

2002; Halpern *et al.* 2008). This has generated a growing demand for fast and cost-effective methods to assess, monitor and mitigate human impacts (Bowen & Depledge 2006; Ugland *et al.* 2008; Reichert *et al.* 2010), as well as to quantify biodiversity and identify areas of conservation priority (Shokri & Gladstone 2009; Mazaris *et al.* 2010). With inadequate

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baseline information on species and reduced availability of taxonomic expertise (Wheeler, Raven & Wilson 2004), there is more incentive to focus on higher taxonomic ranks, which are easier to identify and handle (Beattie & Oliver 1994). Owing to its cost efficiency (Pik *et al.* 2002; Mandelik, Roll & Fleischer 2010), such practice, although still controversial when applied for conservation purposes (Lewandowski, Noss & Parsons 2010), has been widely used over the last two decades (Fig. S1, Supporting Information) for assessing community responses to environmental changes.

A review of the current literature on taxonomic sufficiency (see Materials and methods for further details), which involves the use of higher taxa as surrogates of species (hereafter simply referred as 'taxonomic surrogates'), revealed that the higher-taxon approach has been applied worldwide, from polar to tropical regions, in terrestrial, freshwater, transitional (i.e. estuaries and coastal lagoons) and marine habitats (Fig. S2 and Appendix S1, Supporting Information). Taxonomic sufficiency focused initially on the assessment of human impacts on marine benthic invertebrates, extended rapidly to the assessment of natural gradients of environmental variation (e.g. Wodarska-Kowalczyk & Kędra 2007) and became applied to a wide range of organisms, including plants, algae, invertebrates and vertebrates (Fig. S3, Supporting Information, see also Appendix S1, Supporting Information).

The similarity between community patterns at species level and at higher taxonomic ranks is thought to represent congruencies in community responses across the taxonomic hierarchy (e.g. Olsgaard, Somerfield & Carr 1997; Lovell *et al.* 2007; Heino 2008). This similarity has frequently been measured using Spearman's correlation (ρ), which expresses, in this case, the correlation between pairs of resemblance matrices. Its application to taxonomic surrogates is used to determine the extent to which community patterns at species level are similar to those obtained analysing higher taxa (Somerfield & Clarke 1995). In most cases, genus- and family-level data showed the highest correlations with species-level data and were identified respectively as suitable taxonomic surrogates in more than 80% and in more than 70% of case studies assessing either natural or human-driven variations in assemblages (Fig. S4, Supporting Information).

The use of taxonomic surrogates raised a debate among ecologists, opposing pragmatism (Warwick 1993; Williams, Gaston & Humphries 1997; Dauvin, Bellan & Bellan-Santini 2010) to the inherent risk of causing a loss of ecological information (Maurer 2000; Boero 2001; Terlizzi *et al.* 2003). The main disadvantage of considering higher taxa as proxies of species is that species identities and their relevant ecological information are lost. Therefore, although taxonomic surrogacy could be successful in identifying patterns of community change, concerns might arise because taxonomic surrogates may obfuscate the underlying ecological processes (Somerfield & Clarke 1995; Jones 2008). The success of taxonomic surrogates would rely on the idea that species within higher taxa, especially within genera and families, could encompass some degree of ecological coherence (Warwick 1993). This idea

stems from Darwin's hypothesis (1859) about similarities in habit among congeneric species and has received renewed emphasis with recent developments in phylogenetic niche conservatism (e.g. Webb *et al.* 2002) and tests for phylogenetic signal (Blomberg, Garland & Ives 2003). The assumption that shared evolutionary ancestry can account for shared ecological traits among related species may be strongly violated when extended to taxonomic groups, because taxonomic relationships are not necessarily aligned with phylogenetic relatedness (Wheeler 2004). Moreover, in many cases, ecological similarity among species may not be related to phylogenetic relatedness (Losos *et al.* 2003; Carranza, Defeo & Arim 2011). Several authors have suggested that the way in which species are distributed among higher taxonomic ranks could cause correlations between community response at species and higher taxonomic levels (e.g. Giangrande, Licciano & Musco 2005; Dethier & Schoch 2006; Bevilacqua *et al.* 2009). In this case, higher taxa would be more or less effective as surrogates of species depending on the higher taxa to species ratio (hereafter indicated as $\phi = t/s$, where t is the number of taxa of a given taxonomic rank higher than species, and s is the number of species).

As for most proxies of species diversity (Sætersdal & Gjerde 2011), taxonomic surrogates lack a clear theoretical and ecological foundation to support their effectiveness. This, in turn, is crucial to the understanding of their limits and contexts of application. Here, we explore mechanisms underlying the effectiveness of taxonomic surrogates in community ecology. Specifically, we assess whether the ability of higher taxa to represent species-level community responses could be a result of numerical relationships among species and higher taxa (i.e. ϕ) or might be related directly to taxonomic relatedness among species (i.e. the relative closeness of species in the Linnaean taxonomic hierarchy). We performed four tests aimed at disentangling the mechanisms generating correlations between community patterns at species and higher taxonomic resolution. Our null hypotheses are that (1) similarity between community patterns at species and higher taxonomic level (expressed as ρ) is not correlated with ϕ , (2) ρ values depend on taxonomic relatedness of species, (3) the effectiveness of taxonomic surrogates (i.e. their ability to allow analyses to detect significant variations in the multivariate structure of communities) is not correlated with ρ and finally (4) the effectiveness of taxonomic surrogates in elucidating patterns of community responses to environmental drivers could not be determined on the basis of ϕ .

As a preliminary step, to test hypothesis (1), we performed a web-based review of the peer-reviewed literature on taxonomic surrogacy in the last two decades to check for a possible correlation between ϕ and ρ across different organisms, habitat types and environmental contexts. As literature data were not suitable to test the last three hypotheses, we focused on one of the most diverse and widespread metazoan phyla, the Mollusca, analysing ten of our own data sets of Mediterranean marine assemblages involving several types of habitat and environmental settings.

Materials and methods

LITERATURE REVIEW ON TAXONOMIC SURROGACY

The existing literature on taxonomic surrogacy was searched using *ISI Web of Knowledge*. The search was performed on all available data bases, from 1990 to 2010 inclusive, using the key words 'taxonomic surrogacy', 'taxonomic surrogates', 'taxonomic sufficiency', 'taxonomic resolution', 'higher-taxon' or 'taxonomic aggregation' in the *Topic* field.

A total of 678 unique publications were found. Among these, we selected those providing information on the effectiveness of taxonomic surrogates used for the analyses. Reviews, viewpoints, commentaries and articles not containing actual data on the effectiveness of taxonomic surrogates were excluded. A total of 191 publications remained, reporting a total of 280 case studies (Fig. S2 and Appendix S1, Supporting information). We used all selected case studies to identify the most recurrent sufficient taxonomic levels in investigating variations in either natural or human-driven assemblages. According to the original definition of taxonomic sufficiency (Ellis 1985), a given taxonomic surrogate is effective, or sufficient, when it is suitable to meet the objective of the study. More specifically, we considered as effective those taxonomic surrogates that led analyses to detect significant variations ($\alpha = 0.05$) in assemblage structure (e.g. to detect an impact) consistently with analyses of species-level data. For a minor subset of case studies (<5%), as only multivariate ordination techniques were employed to analyse data, taxonomic surrogates were considered effective when ordination plots were comparable to those obtained at species level, or when $\rho > 0.90$ (if available).

For a subset of 168 case studies of the 280 (Appendix S1, Supporting Information), we were able to extract the number of species (s) and the number of higher taxa (t). Thus, for each taxonomic surrogate, it was possible to calculate the corresponding ϕ value (i.e. the higher taxa/species ratio, t/s). The rate of effectiveness of taxonomic surrogates at decreasing ϕ was determined. All taxonomic surrogates investigated in the 168 case studies were divided according to their own ϕ into ten groups corresponding to ten increasing ranges of ϕ values (i.e. 0–0.1, 0.1–0.2, ..., 0.9–1). Then, for each range of ϕ values, the number of cases in which all taxonomic surrogates were not effective was counted and expressed as a percentage of the total of cases in each group. The rate of effectiveness of taxonomic surrogates was also determined separately for each higher taxonomic rank and expressed as a percentage of ineffective cases on the total number of cases for each taxonomic surrogate (Genus, $n = 107$; Family, $n = 145$; Order, $n = 61$; Class, $n = 50$; Phylum, $n = 44$).

CORRELATION BETWEEN ϕ AND ρ BASED ON LITERATURE DATA

For a subset of 85 case studies of the 280 (Fig. S2 and Appendix S1, Supporting information), we were able to extract ϕ values and correlation values ρ (Spearman's rank correlation) between species and higher-taxon matrices, for each higher taxonomic rank investigated as surrogate of species level. In most studies (>94%), ρ values were calculated between resemblance matrices based on Bray–Curtis similarity/dissimilarity or equivalent distance measures (e.g. Sørensen's similarity) with different data transformations, in most cases (>80%) square root or double square root. A total of 226 (ϕ , ρ) paired values were obtained. Then, ρ values from these case studies were plotted against the corresponding ϕ values. Finally, to test hypothesis (1), a linear regression of $\rho = mx + b$ [where $x = \ln(\phi)$]

was fitted separately for marine invertebrates ($n = 118$), transitional water invertebrates ($n = 31$), freshwater invertebrates ($n = 14$), terrestrial invertebrates ($n = 18$), algae ($n = 39$) and terrestrial plants ($n = 6$). Regression analysis was not attempted for vertebrates because only two points were available. In all regressions, the intercept was set to 1 because at species level $t = s$ and thus $\phi = 1$, $\ln(\phi) = 0$ and because $\rho = 1$, b has to be equal to 1.

DATA SETS ON MARINE MOLLUSC ASSEMBLAGES

For tests 2–4, which needed manipulation of matrices of actual data on assemblage structure, we used ten of our own data sets from previous studies on Mediterranean marine assemblages (see Table S1, Supporting Information). We focused on the phylum Mollusca because (i) it represents one of most diverse and widespread metazoan phylum, (ii) its taxonomy is well known and relatively stable, (iii) it involves both very speciose higher taxa as well as monotypic ones and (iv) several species-level data sets involving different sources of environmental variations and habitat types were available (Table S1, Supporting information).

RANDOM SIMULATION TESTS ON TAXONOMIC SURROGATES

The assumption underlying hypothesis (2) is that high congruence between species and higher taxonomic ranks is due to the fact that species are aggregated according to the specific taxonomic hierarchy used. This would originate from ecological resemblance among species within higher taxa and, consequently, from similar responses to environmental drivers of taxonomically related species. It is expected therefore that the loss of information deriving from aggregating species into higher taxa following the true taxonomic hierarchy is lower than what is expected from randomly aggregating species into higher taxa. To test for this, we constructed a null model based on random simulations in which ρ values between species and higher-taxon matrices were tested against ρ values between species and randomly aggregated matrices. For each mollusc data set, the whole species data matrix was aggregated at higher taxonomic ranks (i.e. Genus, Family, Order and Class) following the true taxonomy. Then, for each matrix, we derived the corresponding among-sample resemblance triangular matrix based on Bray–Curtis similarity. Finally, we calculated the Spearman's rank correlation (ρ) between the triangular matrix at species level and each triangular matrix at higher taxonomic level, as an expression of similarity in community patterns between the species level and taxonomically aggregated matrices (Somerfield & Clarke 1995). For each data set, this procedure was carried out by randomly assigning the original species to higher taxa (thus retaining equal ϕ). For each higher taxonomic rank in each data set, random assignments were repeated 1000 times, obtaining a total of 40 000 randomly aggregated matrices. Finally, ρ values obtained from aggregations following Linnaean taxonomy were tested against the average ($\pm 95\%$ CI, $n = 1000$) of ρ values obtained from randomizations.

We also obtained matrices with decreasing ϕ by randomly aggregating each species into a number of groups defined *a priori*. For each data set, we randomly assigned species to a number of groups reducing the number of original species by decrements of 10. We chose such a progressive reduction because this creates a range of simulated ϕ values that encompass ϕ values occurring in all data sets from species to higher taxonomic ranks up to class. Random assignments were repeated 1000 times for each number of groups in each data set. A total of 97 000 randomized matrices were obtained. For all

randomized matrices in each data set, we ran a distance-based permutational multivariate analysis of variance (PERMANOVA, Anderson 2001) to test for significant effects of the investigated environmental driver on multivariate assemblage structure. All analyses were based on Bray–Curtis similarity with 4999 permutations. Designs for analyses are provided in Table S1 (Supporting information). For each data set, we also calculated ρ values between the species-level matrix and each aggregated matrix, following the procedure previously described.

Our null hypothesis (3) is that the effectiveness of higher taxa (i.e. their ability to allow analyses to detect significant variations in the multivariate structure of assemblages as for species) is not correlated with ρ (i.e. the similarity between assemblage patterns at species and higher taxonomic level). To test for this, for each data set, we calculated Pearson's product moment correlations between all P -values obtained from PERMANOVAs based on randomly aggregated matrices and the corresponding ρ values between species and randomly aggregated matrices. Pearson's correlation values were obtained separately for each data set to avoid any bias because of differences in sample size.

For each data set, ρ values between species and randomly aggregated matrices were plotted against the corresponding ϕ values and a linear regression was fitted to check whether the relationship between ρ and $\ln(\phi)$ followed the model obtained by analysing the global literature data base. All regressions were fitted with an intercept set to 1, as for regressions of literature data. For each data set, one point corresponding to $(\phi_{\min}, \rho_{\min})$ was also considered for regressions, where ϕ_{\min} is the higher taxa to species ratio obtained when all species are aggregated into a single class, and ρ_{\min} is the correlation between the species-level matrix and the matrix where all species are aggregated into a single class.

The assumption underlying hypothesis (4) is that the effectiveness of a given taxonomic surrogate depends strictly on the taxonomic relatedness of species rather than on species aggregation *per se*. Thus, the effectiveness of a given taxonomic surrogate could not be determined on the basis of ϕ . To test this last hypothesis, we obtained for each data set the sufficient aggregation ratio, defined as the ϕ value below which 95% of PERMANOVAs on randomly aggregated matrices were unable to detect significant variations (with $P < 0.05$ or lower) in the assemblage imputable to the investigated environmental driver. Then, for each data set, we ran PERMANOVAs based on matrices aggregated following the true taxonomy (i.e. from species up to class level)

to identify the sufficient taxonomic level for analyses, defined as the coarsest taxonomic resolution allowing analyses to detect significant variations in assemblage structure imputable to the investigated environmental driver with $P < 0.05$ or lower. Finally, we checked whether ϕ values of sufficient taxonomic surrogates based on true taxonomic aggregations were consistent with sufficient ϕ values obtained from random aggregations. All analyses used R (www.r-project.org).

Results

CORRELATION BETWEEN ϕ AND ρ BASED ON LITERATURE DATA

The analysis of the literature data showed that the correlation between species and higher taxonomic level community patterns (expressed as ρ) was significantly related to the higher taxa/species ratio (ϕ) (Table 1). Regression analyses showed that the decrease in ρ value against ϕ followed a semilog model consistent across all types of organisms (Fig. 1a, Table 1). Literature data also showed that, independently of the investigated taxonomic level (Table 2), the rate of effectiveness of taxonomic surrogates was very low for $\phi < 0.4$. Taxonomic surrogates accounting for higher ϕ values were generally effective (Fig. 1b).

Table 1. Results of regression analyses of species higher rank matrix correlation (ρ) against corresponding higher taxa/species ratios (ϕ) from literature data, separated for each type of organisms

Type of organisms	Estimate	SE	P	Adjusted R^2
Marine invertebrates	0.105	0.006	< 0.001	0.680
Transitional invertebrates	0.178	0.017	< 0.001	0.752
Freshwater invertebrates	0.133	0.021	< 0.001	0.676
Terrestrial invertebrates	0.114	0.014	< 0.001	0.730
Algae	0.117	0.012	< 0.001	0.650
Plants	0.179	0.030	< 0.001	0.674

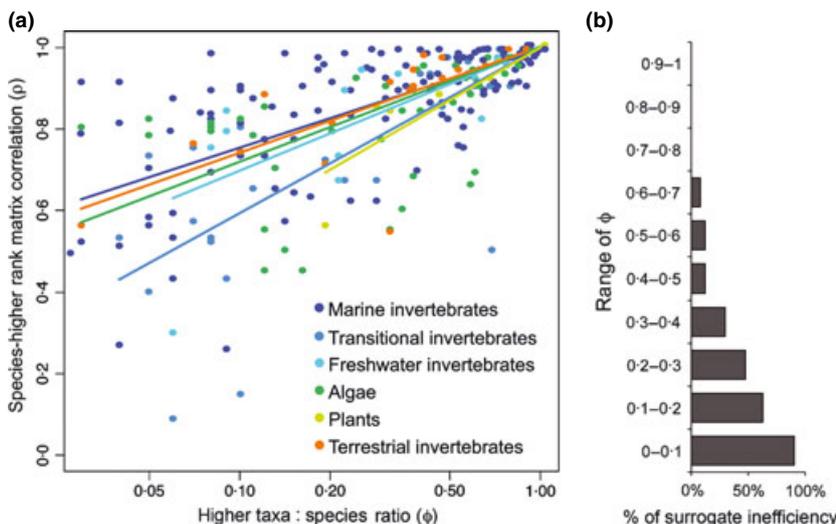


Fig. 1. (a) Semilog plot of Spearman's rank correlation (ρ) between species and higher-taxon matrices against the corresponding ϕ values, from literature case studies on taxonomic surrogates separated for each organism type (i.e. marine, freshwater, transitional, and terrestrial invertebrates, algae, and plants). (b) Percentage of ineffective taxonomic surrogates for each range of ϕ values.

Table 2. Effectiveness of different taxonomic surrogates, for each range of ϕ values, based on literature data. Effectiveness was expressed as percentage of ineffective cases on the total of case studies on each taxonomic surrogate

ϕ Range	Genus (%)	Family (%)	Order (%)	Class (%)	Phylum (%)
0–0.1	67	100	92	90	82
0.1–0.2	50	52	54	68	–
0.2–0.3	100	35	67	100	0
0.3–0.4	25	22	67	–	–
0.4–0.5	17	5	0	0	0
0.5–0.6	6	4	0	–	–
0.6–0.7	8	8	–	–	–
0.7–0.8	0	0	–	–	–
0.8–0.9	0	0	–	–	–
0.9–1.0	0	0	–	–	–

RANDOM SIMULATION TESTS ON MOLLUSC DATA SETS

We found that, for a given ϕ value, ρ values of species vs. higher taxonomic level data matrices largely fell within the 95% confidence interval of randomly aggregated matrices (Fig. 2, see also Table S2, Supporting Information). However, ρ values from the observed data fell below the 95% confidence interval for a few data sets (Fig. 2, Table S2, Supporting Information).

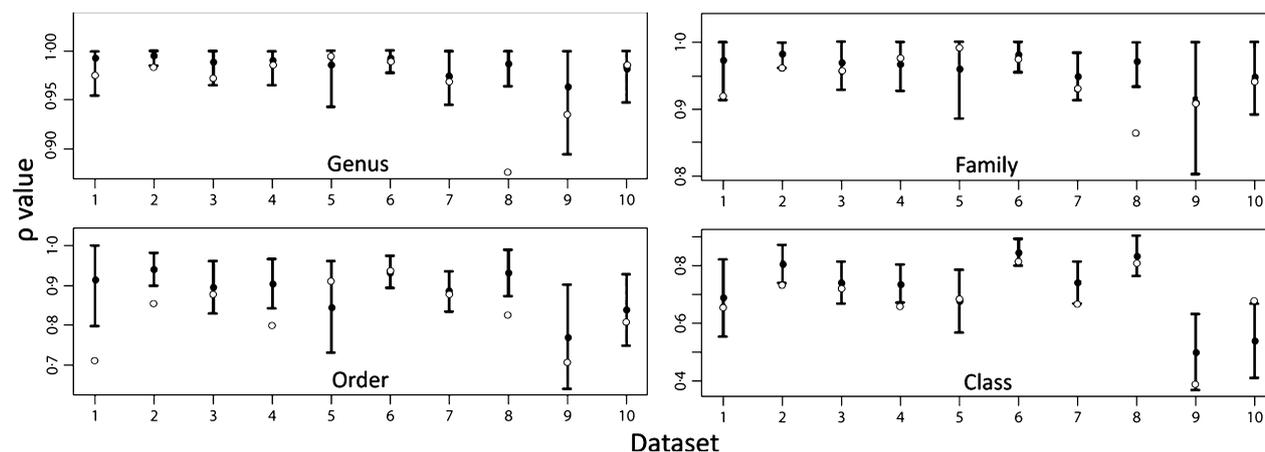


Fig. 2. Spearman's rank correlation ρ values between species matrix and matrices aggregated at higher taxonomic ranks (i.e. Genus, Family, Order and Class) for each of the ten analysed mollusc data sets (white points). In black, mean \pm 95% confidence interval ($n = 1000$) of ρ values between species matrix and matrices aggregated by randomly assigning species to higher taxa.

Table 3. Pearson's product moment correlation between ρ values from random aggregations of species variables and corresponding P -values obtained from multivariate analyses on randomly aggregated matrices for each data set

Correlation	Data set									
	1	2	3*	4*	5	6	7	8*	9	10
(\pm SE)	–0.879 (\pm 0.004)	–0.950 (\pm 0.002)	–	–	–0.555 (\pm 0.025)	–0.637 (\pm 0.010)	–0.698 (\pm 0.012)	–	–0.526 (\pm 0.014)	–0.138 (\pm 0.014)
P	<0.001	<0.001	–	–	<0.001	<0.001	<0.001	–	<0.001	<0.001

*Correlation was not calculated because in these case studies multivariate analyses did not detect significant variations related to the investigated natural or human-driven changes for any taxonomic level.

For all data sets showing significant variation in species-level assemblage structure related to the investigated environmental drivers, a significant negative correlation between P -values obtained from multivariate analyses on randomly aggregated matrices and corresponding ρ values was found (Table 3). In all cases except one (data set 10), the Pearson's product moment correlation was >0.5 , indicating that the ability of the analyses to detect changes induced by natural or human-driven forcing in the multivariate patterns of assemblages was strongly correlated with the information contained in randomly aggregated matrices (i.e. ρ).

Consistent with the results from the literature data (Fig. 1), regression analyses on mollusc data sets showed that reductions in ρ at decreasing simulated ϕ followed a model invariant across different environmental contexts (Fig. 3 and Table 4). The sufficient taxonomic levels obtained from analyses carried out on matrices aggregated following the true taxonomic hierarchy were consistent with the sufficient aggregation levels predicted using random aggregations (Fig. 3 and Table 5). The information contained in randomly aggregated matrices could therefore still depict the ecological responses of assemblages at true decreasing taxonomic resolution. It is worth noting that for data sets 1, 2 and 9, assemblage variation was still detectable at ϕ values lower than those characterizing the identified sufficient taxonomic levels (Fig. 3). This indicates that taxonomic surrogates are effective when the corresponding ϕ

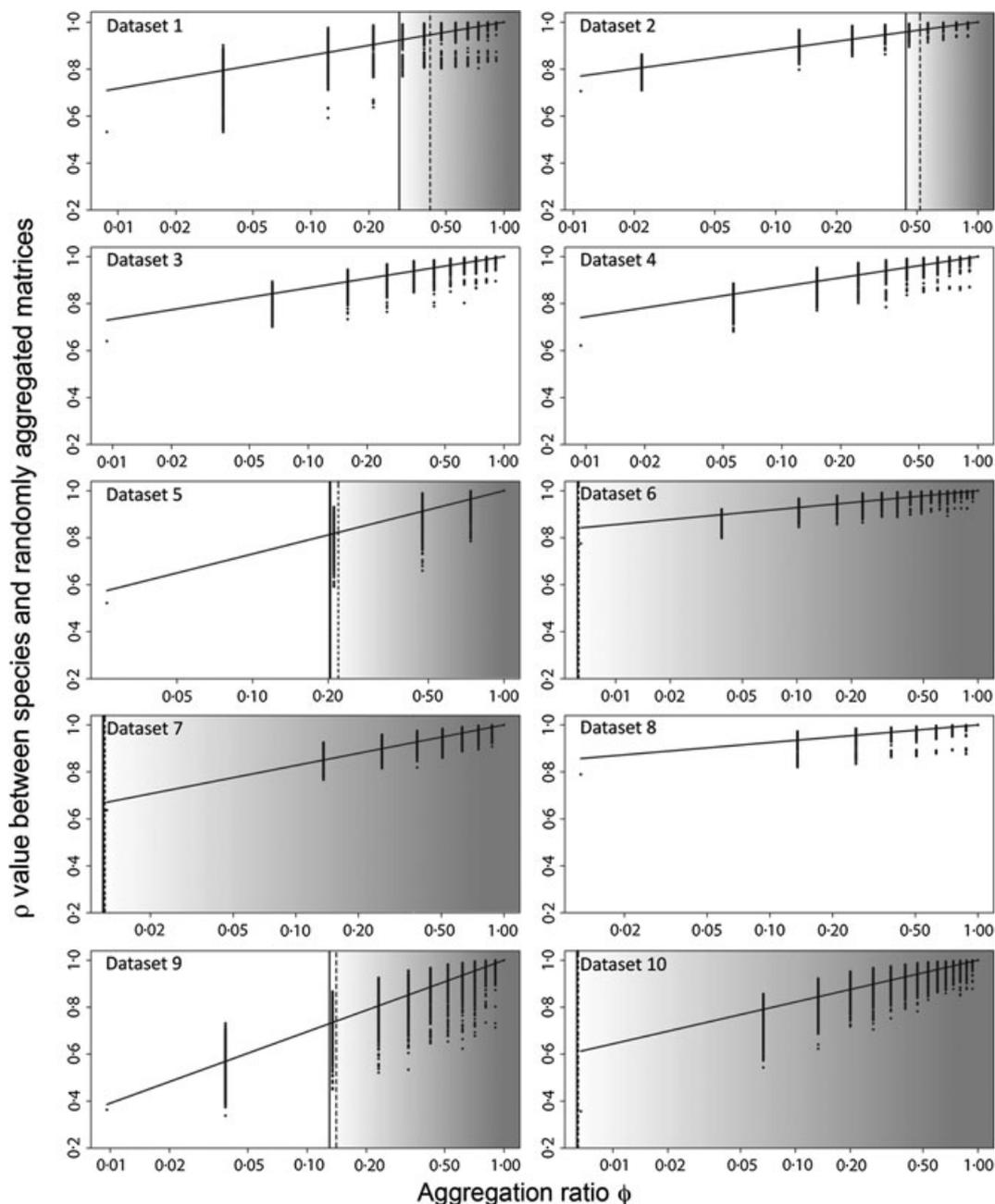


Fig. 3. Semilog plot of ρ values between species matrix and randomly aggregated matrices against the corresponding ϕ values. Fading grey zones indicate the range of ϕ values at which analyses were able to detect significant variations in the multivariate structure of assemblages, whereas dotted lines represent the ϕ values corresponding to the sufficient taxonomic resolution. For data sets 3, 4 and 8, analyses did not show any significant differences attributable to the investigated source of variation neither at species nor at higher true or simulated taxonomic aggregation levels.

values fall within the range of ϕ values that allow the retention of assemblage responses to environmental drivers. Thus, the performance of a given taxonomic surrogate depends on species' aggregation *per se* rather than strictly on the taxonomic resolution employed.

Discussion

Many ecological theories have been formulated to explain the general effectiveness of taxonomic surrogates of species in

elucidating community responses to human perturbations. The unifying assumption is that natural variability is likely to drive community changes by species replacement, whereas anthropogenic impacts probably are more prone to cause variation in community structure at even higher taxonomic levels (Warwick 1988, 1993; Ferraro & Cole 1990). Long-term human impacts could generate a 'hierarchical response to stress' in organisms (Ferraro & Cole 1990), determining effects at individual or species level at the beginning and, as the disturbance persists and/or increases, affecting even higher taxa. On

Table 4. Results of linear regression analyses of ρ values between species matrix and randomly aggregated matrices against corresponding aggregation ratios (ϕ)

Data set	Estimate	SE	<i>P</i>	Adjusted <i>R</i> ²
1	0.061	< 0.001	< 0.001	0.997
2	0.051	< 0.001	< 0.001	0.999
3	0.058	< 0.001	< 0.001	0.999
4	0.056	< 0.001	< 0.001	0.999
5	0.117	0.001	< 0.001	0.997
6	0.031	< 0.001	< 0.001	1.000
7	0.075	< 0.001	< 0.001	1.000
8	0.033	< 0.001	< 0.001	1.000
9	0.132	< 0.001	< 0.001	0.996
10	0.077	< 0.001	< 0.001	0.999

the other hand, species could be unable to rapidly evolve compensatory responses to human impacts that, unlike natural environmental variation (e.g. seasonality), may easily propagate from species to higher taxa (De Biasi, Bianchi & Morri 2003). However, these explanations are weakened by the growing body of evidence that suggests that natural variation also affects community structure at higher taxonomic levels (e.g. Dethier & Schoch 2006; Heino & Soininen 2007; La Torre-Cuadros, Herrando-Pérez & Young 2007; Lovell *et al.* 2007). Our analysis of previously published surrogacy patterns showed comparable effectiveness of higher taxonomic rank in depicting community response to either natural or anthropogenic environmental variations, at least up to family level. Several studies have found that fine taxonomic resolution (i.e. below family level) is required for the detection of subtle human impacts (e.g. Grimbacher, Catterall & Kitching 2008), whereas

effects of strong natural environmental perturbation can be still detectable at lower (i.e. above family level) taxonomic resolution (e.g. Wodarska-Kowalczyk & Kędra 2007). Such findings suggest that the detection of changes to community structure at different taxonomic resolutions could be related to the strength of perturbations. Taxonomic aggregation is more likely to eclipse subtle effects of a weak perturbation on community structure rather than drastic community changes induced by a strong disturbance, whether natural or human driven. In this light, the strength of a perturbation could partially determine the extent to which taxonomic aggregation can be performed without major loss of information, but does not provide an exhaustive explanation of the effectiveness of taxonomic surrogates. For instance, it does not explain why genus- and family-level identifications, independently of the features of the source of variation, are generally effective in identifying community responses (e.g. Bevilacqua *et al.* 2009; Terlizzi *et al.* 2009).

The bulk of previous empirical evidence on taxonomic surrogacy supported the general idea that higher taxa, especially families, are likely to represent ecologically and functionally homogeneous groups of species (Warwick 1993; Wodarska-Kowalczyk & Kędra 2007; Terlizzi *et al.* 2009). At the rank of family, shared ecological and/or functional traits among species within higher taxa could lead to similar responses to environmental variation. However, the extent to which taxonomic relatedness implies similar ecological traits among species is open to discussion, and generalizations are not unambiguously supported. Species within the same genus or family could show large differences in ecological or functional traits and as a consequence exhibit strong heterogeneity in ecological responses to natural or human-induced changes (Lenat & Resh 2001; Heino & Soininen 2007).

Table 5. Values of ϕ , for each taxonomic rank, based on true taxonomic aggregation, and sufficient ϕ values based on random aggregations of species. The sufficient taxonomic resolution for analyses and the sufficient taxonomic resolution predicted basing on random aggregation models are provided

Data set	<i>s</i>	Value of ϕ based on taxonomic hierarchy					Sufficient ϕ based on random aggregations		
		Species	Genus	Family	Order	Class	Sufficient taxonomic level	Sufficient aggregation ratios	Model prediction of sufficient taxonomic level
1	114	1**	0.816**	0.439*	0.158 ^{ns}	0.026 ^{ns}	Family	0.298	Family
2	92	1*	0.837*	0.533*	0.185 ^{ns}	0.033 ^{ns}	Family	0.456	Family
3†	107	1 ^{ns}	0.766 ^{ns}	0.505 ^{ns}	0.159 ^{ns}	0.028 ^{ns}	–	–	–
4†	106	1 ^{ns}	0.774 ^{ns}	0.462 ^{ns}	0.151 ^{ns}	0.028 ^{ns}	–	–	–
5	38	1**	0.868**	0.684**	0.263**	0.079 ^{ns}	Order	0.263	Order
6	156	1***	0.698***	0.391***	0.109***	0.026**	Class	0.026	Class
7	81	1**	0.778**	0.556***	0.210***	0.037*	Class	0.037	Class
8†	79	1 ^{ns}	0.630 ^{ns}	0.395 ^{ns}	0.136 ^{ns}	0.025 ^{ns}	–	–	–
9	104	1***	0.731***	0.471***	0.163***	0.029 ^{ns}	Order	0.135	Order
10	150	1***	0.722***	0.417**	0.126**	0.020*	Class	0.020	Class

ns, not significant.

The number of species *s* and results of multivariate analyses for each aggregation level are also reported.

P* < 0.05; *P* < 0.01; ****P* < 0.001.

†In these case studies, multivariate analyses did not detected significant variations related to the investigated natural or anthropogenic environmental driver for any taxonomic level, thus no sufficient taxonomic level could be found.

The allocation of species into higher taxonomic ranks is based on shared morphological and genetic traits leading to the identification of monophyletic clades, combined with historical allocation constraints. Thus, taxa of the same rank would simply represent separate clades without further equivalence (Bertrand, Pteijel & Rouse 2006), making it implausible to assume that, with the exception of species, any of the Linnaean taxonomic ranks may be unequivocally associated with the ecology, or function, of organisms. Our results do not support a direct relationship between taxonomic relatedness and environmental sensitivity of species. Taxonomic aggregation did not have significant positive effects in retaining species-level information on assemblage patterns, or, if any effect existed, it was neutral or even negative, with respect to that occurring as a consequence of species aggregation *per se*. Therefore, taxa at taxonomic ranks higher than species may not provide ecologically meaningful information because they can behave as random groups of species unlikely to convey consistent responses to natural or human-driven environmental changes. This does not allow us to exclude niche conservatism in closely related species because taxonomic classification of most organisms is still far from being exhaustively incorporated in a phylogenetic framework (Wheeler 2004). It could be argued, for instance, that the presence of many paraphyletic or polyphyletic taxa, which are essentially arbitrary categories, could obscure the putative within-taxon ecological similarity being responsible for the observed patterns. However, the extent to which phylogenetic relatedness implies ecological similarities among species is also far from being clearly understood. Many studies support such relationships (e.g. Webb *et al.* 2002; Wiens & Graham 2005), whereas many others provide direct or indirect evidence that phylogenetic relatedness and ecological similarity among species are often unrelated (see Losos 2008 for a review; Carranza, Defeo & Arim 2011; Mayfield & Levine 2010). Moreover, the interplay between niche conservatism and directional selection could cause patterns of species coexistence indistinguishable from neutral models (Webb *et al.* 2002; Losos 2008; Mayfield & Levine 2010; Uriarte *et al.* 2010), further complicating the matter.

One of the current major areas of intense activity in ecology is finding the linkages between phylogenetic, taxonomic, ecological and functional aspects of biodiversity (Hooper *et al.* 2005; Faith *et al.* 2009). We found that information loss at decreasing taxonomic resolution simply reflects the nested hierarchical structure of the Linnaean taxonomy. This depends on the closeness between the number of species and the number of higher taxa. Thus, decreases in statistical power to detect natural or human-driven changes in assemblages at higher taxonomic levels may rely mostly on the increased aggregation of species and not on the adopted taxonomic resolution. The use of surrogates of species therefore could be based on the sufficient level of aggregation of species irrespective of their taxonomic relatedness. It could be argued that such an approach, while likely to be effective when higher taxa include similar numbers of species, or in the presence of a majority of monotypic taxa, might be unsuitable when the investigated group of organisms involves species that are unevenly distributed

among higher taxa. Nevertheless, we found that the approach is robust to heterogeneous distributions of species of marine molluscs among higher taxa regardless of whether they were speciose or not.

The effectiveness of taxonomic surrogates has been related to the higher taxa/species ratio in several taxonomic groups (e.g. Andersen 1995; Giangrande, Licciano & Musco 2005; Heino & Soininen 2007). Our results on the effectiveness of taxonomic surrogates above certain ranges of ϕ values from the literature suggest that the approach could be generalizable to a wide range of organisms. A note of caution is necessary, however, because sample sizes (i.e. the number of cases from the literature) vary depending on the taxonomic surrogate, because of an underrepresentation of case studies on the effectiveness of taxa higher than family. Moreover, in most of the investigated studies, analyses were based on the Bray–Curtis similarity/dissimilarity index and slight transformations of data (e.g. square root). Further investigation is needed to assess the effect of different resemblance indices and data transformations on the effectiveness of taxonomic surrogates, as well as to broaden the array of investigated organisms, before any generalization may be drawn.

Undoubtedly, there are practical advantages in using a sufficient aggregation level in setting appropriate surrogates of species with respect to more classical higher-taxon approaches. Surrogates based on sufficient aggregation of species variables allow us to overcome problems related to the instability of allocating species into higher taxa. They also allow the insertion of intermediate taxonomic ranks (e.g. superfamilies and infraorders) or the removal of classical ranks. Also, because taxonomic revisions based on cladistic criteria or molecular analyses would imply a reconsideration of Linnaean ranks, such an approach could conciliate the use of taxonomic surrogates with future amendments of species classification schemes. Furthermore, the higher taxa/species ratio may be at the base of a general framework unifying species surrogacy in both environmental and conservation studies, because in the latter, the identification of suitable surrogates of species often concerns numerical relationships between species and higher taxa (e.g. Andersen 1995; Williams, Gaston & Humphries 1997; Balmford, Lyon & Lang 2000). Above all, the most intriguing prerogative of basing species surrogates on the sufficient aggregation level is that there are legitimate alternative groupings, for example mixing morphological, ecological, functional, phylogenetic and taxonomic criteria. The only constraint is to find the sufficient number of groups to perform analyses as powerful as those carried out at species level. This aspect is crucial in helping ecologists to fully exploit their own taxonomic skills and ecological knowledge of the system being investigated (Groc *et al.* 2010). Focusing on providing detailed resolution for key taxa and coarser resolution for less informative taxa could optimize species surrogacy. This would allow the retention of greater ecological information than when using a single higher taxonomic rank (Lenat & Resh 2001; Jones 2008; Groc *et al.* 2010). In this framework, scientific literature, expertise and analyses of species-level data from pilot surveys could drive the decision of whether to retain high taxonomic detail

(e.g. indicator taxa, sensitive species and identification easiness) or to proceed to aggregations (e.g. difficult taxa and tolerant species).

The major benefit of taxonomic sufficiency is that the use of low taxonomic resolution allows management of limited available taxonomic information, leading to reduced costs and time of procedures associated with fine taxonomic identifications. Reduced time and costs are, however, not absolute and depend on several factors including experimental settings, the intrinsic difficulty of the investigated groups of organisms and the level of taxonomic expertise (Thompson, Riddle & Stark 2003). Therefore, trade-offs between the need for ecological information and taxonomic constraints should be modulated (Jones 2008) and cannot justify ecologists systematically choosing a given taxonomic surrogate as a solution. The convenience of taxonomic surrogates has often been overstated based on the fact that in most cases little information on the life history and ecology of species is available and as a consequence species-level analyses do not necessarily lead to an improved capacity to make inferences about the observed patterns (James, Smith & Fairweather 1995). As the lack of basic information on species ecology and systematics cannot be generalized to all groups of organisms, this could lead to further dismissal of detailed taxonomy. A deeper understanding of the mechanisms underlying ecological processes will only be achieved as a consequence of a major advance in basic disciplines such as autecology and systematics. The method we propose here, based on the 'highest practicable aggregation', could improve upon the use of taxonomic surrogates of species. For decades, species surrogacy has been approached by focusing almost exclusively on taxonomic sufficiency. We have demonstrated that alternative solutions could be practicable and even more profitable.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Summary of literature information.

Table S1. Data set information.

Table S2. Species-aggregated matrix correlations.

Fig. S1. Cumulative number of publications per year.

Fig. S2. World map of literature case studies.

Fig. S3. Percentage of case studies on different organisms.

Fig. S4. Effectiveness of different taxonomic surrogates.

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