Jyväsjärvi, J., **Virtanen, R.**, Ilmonen, J., Paasivirta, L., Muotka, T. (2018):
Identifying taxonomic and functional surrogates for spring biodiversity conservation
Conserv. Biol. **32** (4), 883 – 893

http://dx.doi.org/10.1111/cobi.13101

Identifying taxonomic and functional surrogates for spring biodiversity conservation

Jussi Jyväsjärvi[1], Risto Virtanen[1,2,3], Jari Ilmonen[4], Lauri Paasivirta[5] and Timo Muotka[1,6]

[1] University of Oulu, Department of Ecology and Genetics, P.O. Box 3000, FI-90014, Finland

[2] Department of Physiological Diversity, Helmholtz Center for Environmental Research – UFZ, Permoserstr. 15, Leipzig 04318, Germany

[3] German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Deutscher Platz 5e, Leipzig D-04103, Germany

[4] Metsähallitus, P.O. Box 94, FI-01301, Vantaa, Finland

[5] Ruuhikoskenkatu 17 B 5, FI-20240, Salo, Finland

[6] Finnish Environment Institute, Natural Environment Centre, University of Oulu, P.O. Box 413, FI-90014, Finland

Corresponding author: Jussi Jyväsjärvi
email: jussi.jyvasjarvi@oulu.fi

Keywords: Taxonomic diversity, functional diversity, *Bryum weigelii*, *Paratrichocladius skirwithensis*, *Asellus aquaticus*, *Macropelopia*, complementarity

Running head: Spring biodiversity surrogates

Article Impact Statement:

Cross-taxon complementarity and statistical modeling select surrogates identifying springs of special conservation value, as required by EU Water Framework Directive.

This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the Version of Record. Please cite this article as doi: 10.1111/cobi.13101.

Abstract

Surrogate approaches are widely used to estimate overall taxonomic diversity for conservation planning. Surrogate taxa are frequently selected based on rarity or charisma, while selection using statistical modeling has been rarely applied. We used boosted regression tree models (BRT) fitted to biological data from 165 springs to identify bryophyte and invertebrate surrogates for taxonomic and functional diversity of boreal springs. We focused on these two groups because they are well known and abundant in most boreal springs. According to BRT, the best indicators for taxonomic vs. functional diversity differed: while the bryophyte *Bryum weigelii* and the chironomid larva *Paratrichocladius skirwithensis* best indicated taxonomic diversity, the isopod *Asellus aquaticus* and the chironomid *Macropelopia* spp. were the best surrogates of functional diversity. In a scoring algorithm for priority-site selection, taxonomic surrogates performed only slightly better than random selection for all spring-dwelling taxa, but were very effective in representing spring specialists, providing a distinct improvement over random solution. However, the surrogates for taxonomic diversity performed poorly in representing functional diversity, and vice versa. When combined with cross-taxon complementarity analyses, surrogate selection based on statistical modelling provides a promising approach for identifying groundwater-dependent ecosystems of special conservation value, a key requirement of the EU Water Framework Directive.

Introduction

Complete biodiversity surveys require a formidable effort in terms of time and expenses, as well as great expertise in taxonomic identification. They are therefore largely unattainable and conservation decisions must be based on surrogate measures instead. Taxonomic surrogates are assumed to represent the occurrence and distribution of other biota and, consequently, targeting the limited conservation resources to protect these species should also afford protection to a broad range of other species with similar habitat requirements. In other words, conservation practitioners hope that the ‘known biodiversity is a good surrogate for the unknown’ (Rodrigues & Brooks 2007).

Tests of the efficacy of taxonomic surrogates have yielded variable results. While some studies have shown the surrogate approach to bear great promise (Sergio et al. 2005; Branton & Richardson 2014; Li & Pimm 2016), others have provided only tentative (Rodrigues & Brooks 2007) or no (Bifolchi & Lodé 2005; Ilg & Oertli 2017) support for the concept. These studies have used widely differing definitions of taxonomic surrogates, with some focusing on a few, or even a single, umbrella or focal species, while others have used whole organism groups (often vascular plants or birds; e.g. Larsen et al. 2012) to predict the presence and distribution of other groups (for a review, see Caro 2010). Mac Nally and Fleishman (2004) introduced a completely different approach to the selection of taxonomic surrogates, i.e. modelling-based selection, where empirical data are used to determine indicator species instead of deciding which taxa to use on a priori criteria. An important step in their approach is to confront the candidate indicator species with new, independent test data to validate the model and, ideally, to test if the species selected are transferable to other regions and environmental conditions.

Rarity hotspots are often regarded as key targets for conservation but they do not always coincide with those of overall taxonomic richness (Prendergast et al. 1993). Therefore, the search for surrogate groups should strive primarily to the detection of species whose distributions predict the distributions of other biota (‘cross-taxon complementarity’; Williams et al. 2006; Cabeza et al. 2008). Tests of the success of surrogate species in predicting such complementarity in other biota are, however, scarce and strongly biased towards terrestrial ecosystems (e.g. Franco et al. 2009).

While the preservation of taxonomic richness is important on its own right, other facets of biodiversity may provide complementary insight into priority-site selection. Recent comparisons of taxonomic and functional diversity have suggested relatively weak correspondence between these two aspects of diversity (Devictor et al. 2010; Guareschi et al. 2015). Indeed, surrogate species for taxonomic and functional diversity may be completely different (Sattler et al. 2014) and networks designed to protect taxonomic richness may do poorly in protecting functional diversity. Therefore, the use of functional in addition to taxonomic indicators might prove beneficial in systematic conservation planning (Sattler et al. 2014).

European Water Framework Directive (EC 2000) has greatly improved freshwater management in Europe, while its sister directive, Groundwater Directive (EC 2006), lacks a correspondingly strong biological basis for the protection and management of groundwater resources. Groundwater-dependent ecosystems such as cold-water springs provide numerous ecosystem services (e.g. potable water, crop irrigation) and about 75% of EU citizens depend on groundwater as their primary water supply (Kløve et al. 2011). When groundwater enters land surface, a spring is formed, a groundwater-dependent ecosystem (GDE) that is ecologically closely linked to its terrestrial surroundings (Cantonati et al. 2012). Cold-water (non-thermal) springs are abundant (> 4 springs/km^2; Glazier 2009) throughout the globe. In Finland, for example, there are over 32 000 mapped springs but the actual number is likely much higher. Boreal springs and spring-fed streams host a high number of habitat specialist (i.e. crenophilous) insect and plant species, many of which are endangered (Ilmonen et al. 2012). For example, 12% of the bryophyte species classified as endangered in Finland occur exclusively in springs (Rassi et al. 2010). Similar to most other small water bodies, springs are threatened by a multitude of anthropogenic activities. Chemical contamination impairs groundwater quality and land drainage alters groundwater hydrology, lowering the water table and reducing groundwater discharge into springs (Lehosmaa et al. 2017). As the upmost headwater sites within river networks, springs are isolated aquatic ’islands’ within a terrestrial matrix, with a low degree of connectivity to other similar habitats. This renders springs particularly vulnerable to anthropogenic stressors. Therefore, EU requires member countries to protect the ecosystem services and biodiversity of springs and other GDEs (Kløve et al. 2011). A prerequisite for achieving this goal is to develop methods for a reliable identification of springs of special conservation value.

We tested the applicability of the surrogate-taxa approach to priority-site selection using both taxonomic and functional diversity indicators for boreal springs. For this purpose, we used boosted regression tree modeling on biological data from 116 springs and spring-fed streams in Finland to identify candidate surrogates of taxonomic and functional diversity among bryophyte and invertebrate species. These two groups were selected for the study because, compared to other spring biota, they are relatively well known, easy to sample and typically abundant in boreal springs. We then used independent biological data from 49 springs to test if the priority sites for spring conservation selected using the surrogate(s) predict the priority sites for other spring biota, thus indicating their potential as surrogates for site prioritization in conservation networks. We specifically aimed to identify surrogates for spring-specialist taxa rather than wholesale taxonomic richness, because the latter is likely to contain several headwater generalists for which springs are secondary habitats and are therefore of no special conservation concern.

Methods

Field data

We used bryophyte and benthic invertebrate data from 165 Finnish springs, collected between 1999 and 2009. The sampled springs span a latitudinal range of ca. 1000 km and altitudinal range of 620 m and include all kinds of spring ecosystems ranging from small (0.5 m^2), distinct spring sources to large spring complexes (> 10.000 m^2). The data also include peatland-dominated, glaciofluvial and calcareous springs, resulting in considerable variation in pH of the spring water (range 4.6-8.2). Given the extensive spatial and environmental gradients, our data well represents spring ecosystems in boreal regions. A great majority of sites were unmodified, near-pristine springs, but 10% of the springs suffered from structures for water extraction, logging or land drainage in the vicinity of the spring.

We sampled benthic invertebrates in May to June with a hand-net (mesh size 500 µm) by kicking and sweeping submerged substrates. Sampling was restricted to the first 20 m from the spring source, and all habitat types within that area were sampled. All invertebrates, including chironomid larvae, were identified mainly to species level. However, as some taxa could only be identified to genus (or species group), we retain henceforth the term 'taxonomic richness/diversity'. We sampled spring bryophytes at 1- or 2-m intervals (depending on spring size) from the point of discharge along the main course of the flow in 0.5 × 0.5 m quadrats. The number of plots was usually six, but in the smallest springs only one or two plots could be sampled.

Taxonomic diversity

We used mean standardised taxonomic richness (STR) to measure the 'average' richness of crenophilous invertebrates and bryophytes; it was considered to represent the wholesale taxonomic richness of crenophiles of each study spring. We calculated STR by dividing the observed taxonomic richness by maximum taxonomic richness across all study sites, separately for macroinvertebrates and bryophytes, and then calculating the average of these two standardised richness values for each site. Values close to 1.0 indicate high-diversity sites in terms of taxonomic richness of both invertebrates and bryophytes while values close to zero indicate low taxonomic richness.

Functional diversity: bryophytes

Databases for plant traits contain very few trait data for non-vascular plants. Therefore, we compiled four functional traits that relate to bryophyte growth, reproduction or survival: shoot length, presence of secondary pigments, spore size and growth form. We obtained this information for 89 of the 92 bryophyte species included in our data. Bryophyte shoot length relates strongly to species' competitive ability. Values for this trait were obtained from Hill et al. (2007), except for *Hygrohypnum cochlearifolium* and *Warnstorfia trichophylla*, for which estimates were obtained from herbarium specimens. Spore size contributes to dispersal and local persistence of bryophytes (Virtanen 2014). The average spore size for most species was obtained from Hill et al. (2007). No spore diameter was available for *Barbilophozia quadriloba*, *Hygrohypnum cochlearifolium* and *Warnstorfia trichophylla*, so we used mean across congeneric species as an estimate of spore size for these species. The production of secondary pigments in leaf lamina cell walls protects bryophytes from excess solar radiation (Robinson & Waterman 2014); this trait yielded three categories (no, some or frequent pigmentation). Finally, bryophytes are clonal or colonial organisms and their functioning is strongly linked to growth form, which influences survival, water relations and photosynthesis (Muotka & Virtanen 1995, Ah-Peng et al. 2014). Life forms were obtained from Hill et al. (2007) and they included nine categories. For more detailed description of bryophyte traits, see Supporting Information.

Functional diversity: benthic invertebrates

For invertebrates, we compiled five ecological and biological traits: current preference, feeding type, locomotion type, dispersal capacity and maximal body size (Supporting Information). These traits are key biological characteristics of freshwater invertebrates (Merritt & Cummins 1996), contributing to their life histories, habitat use and feeding behaviour. We obtained most of the trait values from the European trait database (Schmidt-Kloiber & Hering 2015), supplemented by Vieira et al. (2006) and Bis & Usseglio-Polatera (2004). If trait values for a species were unavailable, but were available for other species in the same genus, we used mean trait values across all congeneric species. If trait information was entirely missing for a species/genus, we omitted the species from functional diversity analysis. Species data for the calculation of functional diversity comprised 137 macroinvertebrate taxa. A great majority of taxa with missing trait information were chironomids and other dipterans that occurred in only a few sites, or even a single site.

We used Functional Dispersion (FDis; Laliberté & Legendre 2010) to measure functional diversity of bryophyte and invertebrate assemblages. FDis was first calculated separately for invertebrates and bryophytes on presence/absence data using the 'dbFD' function of the FD package (Laliberté & Shipley 2011) of the R program (R Core Team 2015); then, the mean of invertebrate and bryophyte FDis values were used to characterize the functional diversity of each study site.

Selection of biodiversity surrogates

Species data from the 165 springs comprised 265 invertebrate and 92 bryophyte taxa. However, the majority of taxa in both assemblages were rare, occurring in a few sites only (Supporting Information). Although rare species may be indicative of the conservation value of a spring, their low frequency of occurrence may obstruct the recognition of their indicator value, restricting their application as biodiversity surrogates (Noss 1990). For the selection of potential surrogate taxa, we thus retained only invertebrate and bryophyte taxa occurring in more than 30% of the study sites. Although arbitrary, this threshold provides a good compromise between the inclusion of sufficient (> 30) number of candidate surrogates and exclusion of very rare taxa. This preliminary screening resulted in 27 invertebrate and 7 bryophyte candidate surrogates (see Supporting Information).

We applied boosted regression trees (BRT) to screen the most potential taxonomic and functional surrogates among the 34 selected invertebrate and bryophyte taxa. In BRT, regression tree modelling (RT) is combined with boosting methods. RT uses one explanatory variable at a time to split observations into two groups (tree leaves) with maximal within-group homogeneity. Tree size is hierarchically increased by repeated splits of the groups formed in the previous step until an overlarge tree is developed. Boosting improves accuracy of the model, as it is easier to find and average many rough rules of thumb than a single, highly accurate prediction rule (Schapire 2003). In boosting, models (e.g. regression trees) are iteratively fitted to training data, gradually increasing emphasis on observations modelled poorly by the existing collection of trees. The final BRT model is thus a linear combination of many trees (usually hundreds to thousands) that can be thought of as a regression model where each term is a tree (Friedman 2001).

Prior to BRT model development, we subdivided our data into two categories. About 70% (n = 116) of the sites were randomly selected for calibration of the BRT models (i.e. training data) and the remaining 49 sites (30%) were assigned to independent ‘TEST’ sites. BRT models were then fitted to training data by using presence/absence of the 34 candidate taxa as predictor variables and STR and FDis as response variables. Gaussian error distribution was assumed for both models and the number of interactions in the models were set to one (i.e. additive model).

Predictor variable (here, taxa) selection in BRT modelling is based on the relative influence (RI) of each predictor (see Elith et al. 2008). RI of each variable is scaled to sum up to 100, with higher values indicating stronger influence of a variable. We used RI as an indicator of surrogate potential – a well-performing surrogate should be included in several tree models and should have a disproportionately high RI compared to remaining taxa. The settings used in the BRT model are given in Supporting Information. Performance of the final model was validated using a three-fold cross-validation process (Elith et al. 2008), and the cross-validated RIs of each taxon were used as the measure of a species potential as a surrogate of taxonomic or functional diversity. We developed the BRT models using gbm package (Ridgeway 2015) of the R statistical program (R Core Team 2015).

Evaluation of surrogate performance

We selected the first two taxa with the highest RI as candidate surrogates for both taxonomic and functional diversity. Using all recorded invertebrate and bryophyte taxa, we then compared the differences in taxonomic and functional richness among the 49 TEST sites categorized based on the presence of the surrogates: (i) no surrogate taxa present, (ii) one surrogate or (iii) both surrogates present. As our study springs harbour many generalist lotic and lentic taxa, we conducted separate analyses for the generalists and for spring specialists (crenophiles; taxa preferring springs and spring-fed streams; see Ulvinen et al. 2002). We thus assessed if the occurrence of the selected surrogates indicates taxonomically (taxonomic surrogates) or functionally (functional surrogates) diverse springs. We also tested if taxonomic surrogates could be used to identify functionally diverse springs, and vice versa. Therefore, we compared differences in taxonomic and functional richness among TEST sites grouped by the presence of taxonomic or functional surrogates. These tests were run using generalized linear models (GLM) with either poisson (taxonomic diversity) or gaussian (FDis) error distributions.

Next, we used Non-Metric Multidimensional Scaling (NMDS) ordination to visualize gradients in invertebrate assemblages of the TEST sites, grouped according to the occurrence of the taxonomic or functional surrogates. Bryophyte ordinations did not show any clear and interpretable community patterns in relation to site groupings and are therefore not presented here. The NMDS was run using Sørensen dissimilarities based on presence/absence data using *metaMDS* function of the vegan package. To test if species composition differed among TEST site groups we used permutational (9999 permutations) multivariate analysis of variance (perMANOVA; function *adonis* in vegan; Oksanen et al. 2015). We examined the relationship of species ordination with key environmental gradients by fitting environmental vectors onto the ordination space using the vegan function *envfit*. Significance of the fitted vectors was assessed using a permutation procedure (9999 permutations) (Oksanen et al. 2015).

To test if the complementarity of the surrogates in priority-site selection represents the complementarity of other spring biota we used a scoring index, rarity-weighted richness (RWR), which provides a rarity value for a species as the inverse of the number of sites where it occurs. Then, the rarity scores of all species at a site are summed to yield a RWR value for the site. In comparative studies, RWR has performed as efficiently as simulated annealing (Csuti et al. 1997) and heuristic reserve-selection algorithms (Albuquerque & Beier 2015) in priority-site selection. For site prioritization, we followed the protocol of Albuquerque and Beier (2015). We first calculated RWR for each TEST site and then sequentially accumulated sites in relation to their species representation (as indicated by the RWR value). We used (i) all bryophyte and invertebrate taxa (n = 148 taxa) or (ii) crenophilous taxa only (n = 47) to run the scoring algorithm for each of the TEST site combinations. Performance of the surrogates was compared to optimal and random solutions. The former consisted all 49 TEST sites, whereas for the latter, the algorithm was run for randomly selected 12 TEST sites (equal to the average number of TEST sites in each site group), without replacement, and the procedure was repeated 1000 times. A well-performing surrogate should deviate strongly from the random solution and approach the optimal solution.

Results

Selection of surrogate taxa

The boosted regression tree (BRT) model with all 34 candidate surrogate taxa explained 55.2% and 46.4% of the standardized taxon richness in the training and TEST data sets, respectively. The chironomid *Paratrichocladius skirwithensis* and the bryophyte *Bryum weigelii* showed distinctly higher RI values compared to other taxa, suggesting their potential as surrogates of taxonomic diversity of spring ecosystems (Fig. 1a).

The BRT model fitted for functional dispersion (FDis) explained 68.1% and 66.9% of the observed FDis values in the training and TEST data sets, respectively. The isopod *Asellus aquaticus* and the chironomid *Macropelopia* spp. had the highest RI values and were thus selected for further evaluation as functional diversity surrogates (Fig. 1b).

Using surrogates to identify richness hotspots: taxonomic diversity

The 49 TEST sites were classified according to the presence of the two surrogate species: *i*) both surrogates absent ($n = 11$), *ii*) only *B. weigelii* present ($n = 10$), *iii*) only *P. skirwithensis* present ($n = 12$), and *iv*) both species present ($n = 16$). Taxonomic richness of headwater generalist invertebrates differed among the site groups ($F_{3,46} = 5.16$, $p = 0.001$), being higher in sites where both surrogates were absent than in sites occupied by *B. weigelii* ($p < 0.001$) or by both surrogates ($p = 0.005$) (Fig. 2a). Generalist bryophyte richness did not differ among the groups ($F = 0.20$, $p > 0.05$; Fig. 2b). Crenophilous invertebrate and bryophyte richness differed among the groups ($F = 7.30$, $p < 0.001$ and $F = 12.01$, $p < 0.001$, respectively) and were higher in sites with either one or both of the surrogates present than in sites with both surrogates absent (all $p < 0.001$; Fig. 2c and d).

Using surrogates to identify richness hotspots: functional diversity

The 49 TEST sites were divided into four groups according to the occurrence of the two functional surrogates: *i*) both surrogate species absent ($n = 16$), *ii*) only *A. aquaticus* present ($n = 4$), *iii*) only *Macropelopia* present ($n = 13$) and *iv*) both species present ($n = 16$). FDis values differed among site groups ($F_{3,46} = 12.37$, $p < 0.001$), being higher in sites with functional surrogates present, either individually (both $p < 0.001$) or in combination ($p < 0.001$) (Fig. 3). Generalist invertebrate species richness differed strongly among the site groups ($F = 9.87$, $p < 0.001$) and was higher in groups with either or both functional surrogates present (all $p < 0.001$). Generalist bryophytes did not differ among the site groups ($F = 0.80$, $p > 0.05$). Presence of functional surrogates did not indicate higher taxonomic richness of crenophilous invertebrates ($F = 0.20$, $p > 0.05$), but crenophilous bryophyte diversity differed among the groups ($F = 3.90$, $p = 0.008$) and was lower in sites occupied by functional surrogates, individually (both $p \leq 0.01$) or in combination ($p = 0.007$).

Cross-taxon complementarity

Invertebrate assemblages differed consistently in the ordination space when either taxonomic or functional surrogates were used to delineate the spring groups but the two groups of surrogates reacted in contrasting ways to major environmental gradients (Fig. 4). Springs where both taxonomic surrogates were present were more pristine, colder and located at higher latitudes than sites characterized by both functional surrogates (Fig. 4).

Optimal solution in the scoring algorithm required about 20% of the TEST sites to represent 75% of all spring-dwelling taxa (bryophytes and invertebrates combined) whereas randomly selected sites incorporated on average only 55% of species with the same number of sites. Taxonomic surrogates performed only slightly (both species present), or not at all (one surrogate present), better than random selection for all taxa (Fig. 5a), but were very effective in representing crenophilous diversity: particularly the presence of both surrogates provided a distinct improvement over random solution. While the optimal solution represented all specialist taxa in less than 30% of the sites, the same number of random sites captured only 70% of crenophilous mosses and invertebrates (Fig. 5b). The two functional diversity surrogates together performed better than random selection for all spring taxa (Fig. 5c), but were clearly inferior in representing crenophilous spring biodiversity (Fig. 5d).

Discussion

A key question in tests of surrogacy is not the level of spatial overlap between potential surrogates and hotspots of taxonomic richness but the extent to which priority sites selected by the surrogate(s) predict priority sites in a target group, or in overall richness (Williams et al. 2006). Therefore, a useful surrogate should yield a better representation of taxonomic diversity than the same number of randomly selected sites (or species) (Cabeza et al. 2008). We showed that the bryophyte *B. weigelii* and the chironomid *P. skirwithensis* tended to occur in springs with high spring-specialist richness and, more importantly, reflected the complementarity of sites to support high taxonomic richness of spring specialists. Our results further suggest a near-equal surrogacy by these two species, and the best performance was achieved when both species co-occurred. However, using a chironomid larva as an indicator of taxonomic richness might be impractical as it requires specialized taxonomic skills, whereas many bryophytes, including *B. weigelii*, can be identified in the field even by a well-trained non-specialist. This bryophyte species is therefore a promising candidate for the surrogacy of spring-specialist diversity in boreal springs.

Both *B. weigelii* and/or *P. skirwithensis* prefer groundwater-dependent ecosystems as their main habitat (Ulvinen et al. 2002; Ilmonen et al. 2009) and they both have a wide distributional range across Europe and the Holarctic region (Spence 1988; Rossaro et al. 2006). They might therefore act as useful surrogates for spring conservation across broad geographical extents. While flagship umbrella species (sensu Kalinkat et al. 2017) might afford better societal acceptance for conservation, springs rarely contain such species. This emphasizes even more the importance of identifying effective and potentially transferable spring biodiversity indicators. Tests of cross-region transferability of biodiversity surrogates are few but results have suggested little consistency in surrogate performance between regions (Rodrigues & Brooks 2007). Mac Nally & Fleishman (2004) questioned the transferability of even the most effective indicators because models based on specific surrogates are likely to work best in areas with similar climate, topography and species composition as in the region of model origin. Nevertheless, our study does support the use of individual species (or combinations of species with complementary distributions) as biodiversity surrogates, particularly of other range-restricted and rare taxa (Ormerod et al. 2010).

We used BRT models to rank potential surrogates of taxonomic and functional diversity. Although BRT and other machine learning methods are less open to scrutiny than conventional statistical approaches, their flexibility and ability to learn complex patterns between the predictor and response variables makes them particularly useful for ecological data sets. However, the flexibility of BRT models is partly due to a multitude of adjustable model specifications (Elith et al. 2008), which can affect the modelling outcome. We tested several specifications, but their influences on the model outcome were negligible, and in all trial runs the same taxa emerged as the most potential surrogates of taxonomic and functional diversity. Thus, we consider our results robust and independent of model settings.

Our key observation was that the surrogates of functional diversity performed poorly in representing taxonomic diversity, and vice versa. Similarly, Guareschi et al. (2015) found that while the Iberian Peninsula reserve network performed well in providing protection for aquatic beetles, it did much less so in representing functional diversity. In contrast, Strecker et al. (2011) found a relatively high (75%) spatial congruence between priority areas for taxonomic, functional and phylogenetic diversity of the Lower Colorado River fishes. Prioritizing functional diversity in conservation programs might be justifiable as it may provide a link between biodiversity and ecosystem functioning. Indeed, change in ecosystem functions and trait diversity may occur without any changes to species diversity (Mokany et al. 2008). We found surrogates of functional diversity frequently in springs slightly impacted by land use, as indicated by lower habitat integrity and higher water temperature. While lower functional diversity in pristine springs may seem counterintuitive, it likely reflects their harsh thermal conditions that constitute a strong habitat filter allowing only a restricted set of trait combinations to persist. The relationship between disturbance and functional diversity is often negatively monotonic (Mouillot et al. 2013) but recent work has shown that moderate disturbance can increase functional diversity, resulting in a unimodal pattern between the two (Biswas & Mallik 2010). Thus, incorporating only pristine springs into protected area networks may yield unsatisfactory results as regards the protection of functional diversity.

EU Water Framework Directive dictates all member countries to develop methods for a reliable identification of groundwater-dependent ecosystems of special conservation value. As our knowledge about the distribution of taxonomic and functional diversity, as well as the current threat status, of springs and other GDEs is clearly insufficient (Kløve et al. 2011), surrogate approaches are needed to meet the challenges of the Directive. Use of indicators for GDE status assessment and monitoring has been advocated as a means to allow policy makers to identify aspects of groundwater management that require improvements over existing policies (EC 2006). However, current indicator systems are based merely on groundwater quality or quantity, with little consideration of GDE biodiversity and ecosystem functioning (Kløve et al. 2014). The growing demand for groundwater resources may cause conflicts between groundwater exploitation and conservation of GDE biodiversity. However, management of groundwater resources and conservation of GDEs are largely disintegrated and there is thus an obvious need for reliable shortcuts for assessing the potential ecological impacts of groundwater abstraction and other land-use related threats to GDEs and the services they provide. Single-species surrogates may provide a powerful tool for various environmental decision-making processes as they can be used to flag GDEs of the highest conservation priority. Such processes include, for example, authorization of groundwater abstraction, protection of habitats in NATURA 2000 network and implementation of EU strategic environmental assessment (SEA) of public plans and projects with potential environmental impacts. In Finland, regional environmental authorities are currently establishing guidelines for the application of the surrogate-taxa approach for GDE conservation, and its applicability to other environmental contexts awaits to be tested. However, restrictions of taxonomic surrogates also need to be acknowledged. For example, identification of surrogate species may sometimes require special skills which may no longer be available in the current era of taxonomic impediment (or even crisis; Agnarsson et al. 2007, Wheeler 2014), or acquiring such skills may require substantial effort. Furthermore, the two taxonomic surrogates identified by us performed poorly in indicating the diversity of generalist bryophytes and invertebrates. Environmental changes (e.g. land drainage; altered thermal conditions) may be less harmful, or even beneficial, for headwater generalists, resulting in higher overall but reduced native diversity in altered GDEs (Jyväsjärvi et al. 2015). However, these generalist taxa are not the targets of GDE conservation but the limited resources should instead aim at protecting the most valuable component of GDE biodiversity, the spring specialist fauna and flora; for that purpose, our approach shows considerable promise.

Acknowledgments

We thank Jari Oksanen for providing help with the complementarity algorithms. We also appreciate the insightful comments by the Handling Editors and three anonymous reviewers on a previous draft of our article. This work was carried out as part of the GENESIS project on groundwater systems (http://www.thegenesisproject.eu) financed by the European Commission 7FP contract 226536. The study was also funded by the Academy of Finland (projects number 128377 and 263601).

Supporting Information

A list of trait categories (Appendices S1 and S2), details on the selection of surrogate taxa (Appendix S3), and settings of the boosted regression trees (Appendix S4) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

Literature cited

Ah-Peng C, Flores O, Wilding N, Bardat J, Marline L, Hedderson TA, Strasberg D. 2014. Functional diversity of subalpine bryophyte communities in an oceanic island (La Réunion). Arctic, Antarctic, and Alpine Research **46**:841-851.

Albuquerque F, Beier P. 2015. Rarity-weighted richness: A simple and reliable alternative to integer programming and heuristic algorithms for minimum set and maximum coverage problems in conservation planning. PLOS One **10**:e0119905.

Agnarsson I, Kuntner M. 2007. Taxonomy in a changing world: seeking solutions for a science in crisis. Systematic Biology **56:**531-539.

Bifolchi A, Lodé T. 2005. Efficiency of conservation shortcuts: an investigation with otters as umbrella species. Biological Conservation **126**:523-527.

Bis B, Usseglio-Polatera P. 2004. Species traits analysis: The application of species trait analysis to the establishment of reference conditions and the assessment of Ecological Status for the implementation of the Water Framework Directive. The STAR Project Deliverables N2 1.

Biswas SR, Mallik AU. 2010. Disturbance effects on species diversity and functional diversity in riparian and upland plant communities. Ecology **91**:28-35.

Branton MA, Richardson JS. 2014. A test of the umbrella species approach in restored floodplain ponds. Journal of Applied Ecology **51**:776-785.

Cabeza M, Arponen A, Van Teeffelen A. 2008. Top predators: hot or not? A call for systematic assessment of biodiversity surrogates. Journal of Applied Ecology **45**:976-980.

Cantonati M, Füreder L, Gerecke R, Jüttner I, Cox EJ. 2012. Crenic habitats, hotspots for freshwater biodiversity conservation: toward an understanding of their ecology. Freshwater Science **31**:463–480.

Caro T. 2010. Conservation by proxy: indicator, umbrella, keystone, flagship, and other surrogate species. Island Press.

Csuti B, et al. 1997. A comparison of reserve selection algorithms using data on terrestrial vertebrates in Oregon. Biological Conservation **80**:83–97.

Devictor V, Mouillot D, Meynard C, Jiguet F, Thuiller W, Mouquet N. 2010. Spatial mismatch and congruence between taxonomic, phylogenetic and functional diversity: the need for integrative conservation strategies in a changing world. Ecology Letters **13**:1030-1040.

EC 2000. Directive 20000/60/EC of the European Parliament and of the council establishing a framework for community action in the field of water policy. Official Journal of the European Communities, L, 327/1.

EC 2006. Directive 2006/118/EC of the European Parliament and of the Council of 12 December 2006 on the protection of groundwater against pollution and deterioration. Official Journal of the European Union, L, 372.

Elith J, Leathwick JR, Hastie T. 2008. A working guide to boosted regression trees. Journal of Animal Ecology **77**:802–813.

Franco A, Anderson BJ, Roy DB, Gillings S, Fox R, Moilanen A, Thomas CD. 2009. Surrogacy and persistence in reserve selection: landscape prioritization for multiple taxa in Britain. Journal of Applied Ecology **46**:82–91.

Friedman JH. 2001. Stochastic gradient boosting. Computational Statistics & Data Analysis **38**:376–378.

Glazier DS. 2009. Springs. Pages 734–755 in GE Likens (editor). Encyclopedia of inland waters. Volume 1. Academic Press Elsevier, Oxford, UK.

Guareschi S, Bilton DT, Velasco J, Millán A, Abellán P. 2015. How well do protected area networks support taxonomic and functional diversity in non-target taxa? The case of Iberian freshwaters. Biological Conservation **187**:134-144.

Hill MO, Preston CD, Bosanquet SDS, Roy DB. 2007. BRYOATT - attributes of British and Irish mosses, liverworts and hornworts with information on native status, size, life form, life history, geography and habitat. Centre for Ecology and Hydrology 88 p.

Ilg C, Oertli B. 2017. Effectiveness of amphibians as biodiversity surrogates in pond conservation. Conservation Biology **31:**437-445.

Ilmonen J, Paasivirta L, Virtanen R, Muotka T. 2009. Regional and local drivers of macroinvertebrate assemblages in boreal springs. Journal of Biogeography **36**:822–834.

Ilmonen J, Mykrä H, Virtanen R, Paasivirta L, Muotka T. 2012. Responses of spring macroinvertebrate and bryophyte communities to habitat modification: community composition, species richness, and red-listed species. Freshwater Science **31**:657–667.

Jyväsjärvi J, et al. 2015. Climate-induced warming imposes a threat to north European spring ecosystems. Global Change Biology **21**:4561-4569.

Kalinkat G, et al. 2017. Flagship umbrella species needed for the conservation of overlooked aquatic biodiversity. Conservation Biology **31**:481-485.

Kløve B, et al. 2011. Groundwater dependent ecosystems. Part II. Ecosystem services and management in Europe under risk of climate change and land use intensification. Environmental Science & Policy **147**:782-793.

Kløve B, et al. 2014. Climate change impacts on groundwater and dependent ecosystems. Journal of Hydrology **518**:250-266.

Laliberté E, Legendre P. 2010. A distance-based framework for measuring functional diversity from multiple traits. Ecology **91**:299-305.

Laliberté E, Shipley B. 2011. FD: measuring functional diversity from multiple traits, and other tools for functional ecology. R package version 1.0-11.

Larsen FW, Bladt J, Balmford A, Rahbek C. 2012. Birds as biodiversity surrogates: will supplementing birds with other taxa improve effectiveness?. Journal of Applied Ecology **49**:349-356.

Lehosmaa K, Jyväsjärvi J, Virtanen R, Rossi PM, Rados D, Chuzhekova T, Markkola AM, Ilmonen J, Muotka T. 2017. Does habitat restoration enhance spring biodiversity and ecosystem functions? Hydrobiologia **793**:161-173.

Li BV, Pimm SL. 2016. China's endemic vertebrates under the protective umbrella of the giant panda. Conservation Biology **30**:329-339.

Mac Nally R, Fleishman E. 2004. A successful predictive model of species richness based on indicator species. Conservation Biology **18**:646–654.

Merritt RW, Cummins KW. 1996. An Introduction to the Aquatic Insects of North America. Kendall Hunt.

Mokany K, Ash J, Roxburgh S. 2008. Functional identity is more important than diversity in influencing ecosystem processes in a temperate native grassland. Journal of Applied Ecology **96**:884-893.

Mouillot D, Graham NA, Villéger S, Mason NW, Bellwood DR 2013. A functional approach reveals community responses to disturbances. Trends in Ecology & Evolution **28**:167-177.

Muotka T, Virtanen R. 1995. The stream as a habitat templet for bryophytes: species' distributions along gradients in disturbance and substratum heterogeneity. Freshwater Biology **33**:141-160.

Noss RF. 1990. Indicators for monitoring biodiversity: a hierarchical approach. Conservation Biology **4**:355–364.

Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Wagner H. 2015. vegan: Community ecology package. R package version 2.3-2.

Ormerod SJ, Durance I, Terrier A, Swanson AM. 2010. Priority wetland invertebrates as conservation surrogates. Conservation Biology **24**:573-582.

Prendergast JR, Quinn RM, Lawton JH, Eversham BC, Gibbons DW. 1993. Rare species, the coincidence of diversity hotspots and conservation strategies. Nature **365**:335–337.

R Core Team 2015. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria

Rassi P, Hyvärinen E, Juslén A, Mannerkoski I. 2010. The 2010 red list of Finnish species. Ministry of the Environment, Finnish Environment Institute, Helsinki

Ridgeway G. 2015. gbm: Generalized boosted regression models. R package version 2.1.1.

Robinson SA, Waterman MJ. 2014. Sunsafe bryophytes: photoprotection from excess and damaging solar radiation. Pages 113-130 in Hanson DT, Rice SK. (eds.). Photosynthesis in Bryophytes and Early Land Plants. Springer, Netherlands.

Rodrigues AS, Brooks TM. 2007. Shortcuts for biodiversity conservation planning: the effectiveness of surrogates. Annual Review of Ecology, Evolution, and Systematics **38**:713-737.

Rossaro B, Lencioni V, Boggero A, Marziali L. 2006. Chironomids from Southern Alpine running waters: ecology, biogeography. Hydrobiologia **562**:231–246.

Sattler T, Pezzatti GB, Nobis MP, Obrist MK, Roth T, Moretti M. 2014. Selection of multiple umbrella species for functional and taxonomic diversity to represent urban biodiversity. Conservation Biology **28**:414-426.

Schapire R. 2003. The boosting approach to machine learning – an overview. Pages 1-23 in Denison DD, Hansen MH, Holmes C, Mallick B, Yu B (eds). MSRI Workshop on Nonlinear Estimation and Classification. Springer, New York.

Schmidt-Kloiber A, Hering D. 2015. www.freshwaterecology.info - An online tool that unifies, standardises and codifies more than 20,000 European freshwater organisms and their ecological preferences. Ecological Indicators **53**:271-282.

Sergio F, Newton I, Marchesi L. 2005. Top predators and biodiversity. Nature **436**:192.

Spence JR. 1988. Bryum Hedw. (Bryaceae) in western North America. Bryologist **91**:73–85.

Strecker AL, Olden JD, Whittier JB, Paukert CP. 2011. Defining conservation priorities for freshwater fishes according to taxonomic, functional, and phylogenetic diversity. Ecological Applications **21**:3002-3013.

Ulvinen T, Syrjänen K, Anttila S. 2002. Bryophytes of Finland: distribution, ecology and red list status. Finnish Environment Institute Reports, Helsinki.

Vieira NK, Poff NL, Carlisle DM, Moulton SR, Koski ML, Kondratieff BC. 2006. A database of lotic invertebrate traits for North America. US Geological Survey Data Series, **187**:1-15.

Virtanen R. 2014. Diaspore and shoot size as drivers of local, regional and global bryophyte distributions. Global Ecology and Biogeography **23**:610-619.

Wheeler Q. 2014. Are reports of the death of taxonomy an exaggeration? New Phytologist **201**:370-371.

Williams P, Faith D, Manne L, Sechrest W, Preston C. 2006. Complementarity analysis: mapping the performance of surrogates for biodiversity. Biological Conservation **128**:253-264.

Figure legends

Figure 1. Relative influence values for the 34 candidate taxonomic (a) and functional (b) surrogate taxa included in the boosted regression tree models. In both cases, the two best-performing taxa (dark bars) were selected for further analyses.

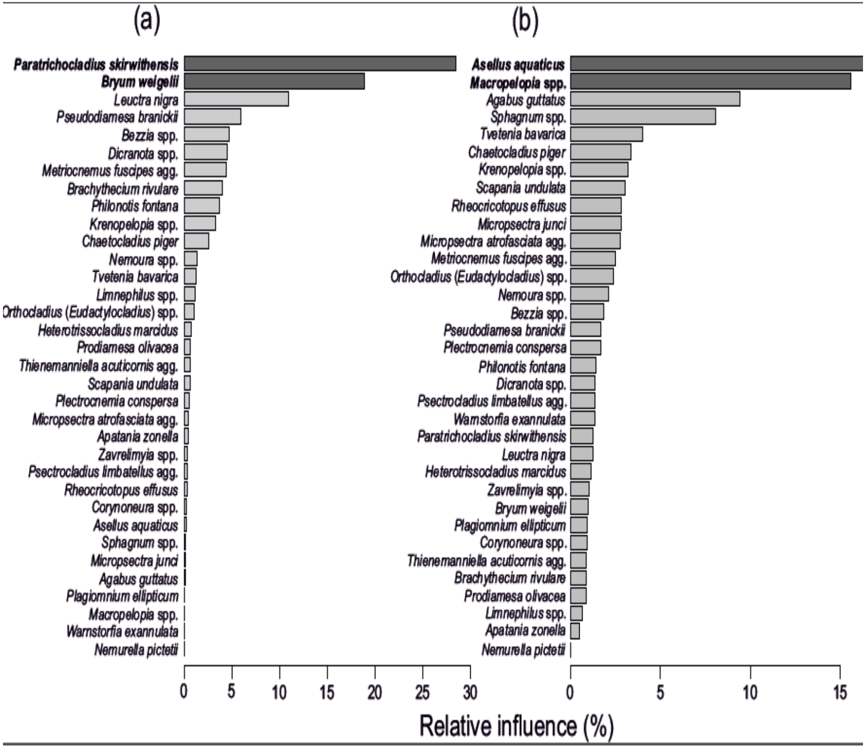


Figure 2. Box-and-whisker plots for generalist macroinvertebrate (a) and bryophyte (b) richness and crenophilous macroinvertebrate (c) and bryophyte (d) richness among the 49 TEST sites with the two taxonomic surrogates (*B. weigelii* and *P. skirwithensis*) absent or present. Boxes represent median values with interquartile range; lower and upper whiskers represent minimum and maximum values, respectively.

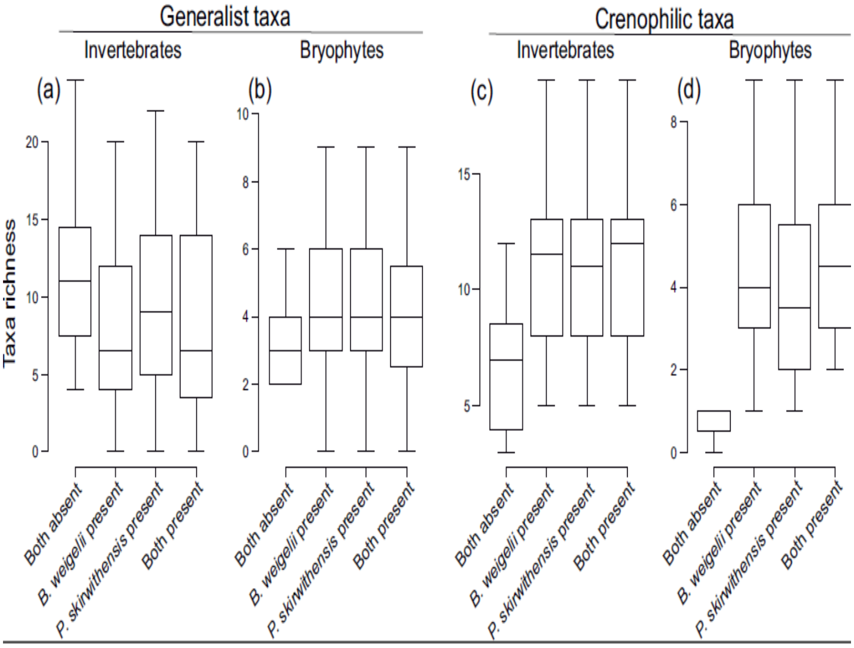


Figure 3. Box-and-whisker plots for the mean functional dispersion values among the 49 TEST sites with the two functional surrogates (*A. aquaticus* and *Macropelopia* spp.) absent or present.

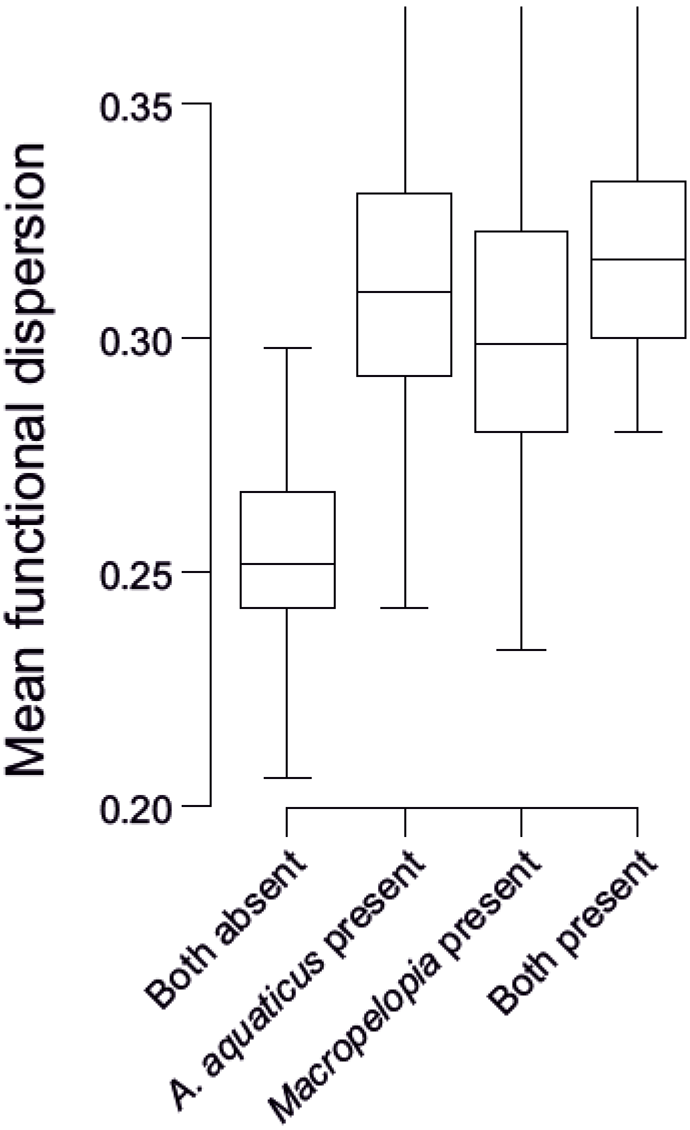


Figure 4. NMDS ordinations of invertebrate assemblages of the 49 TEST sites. Solid-line ellipses represent standard deviations of the point scores of springs occupied by neither or both of the surrogate species, while dashed lines represent springs occupied by one of the surrogates. (a) Taxonomic; (b) functional surrogates. Key environmental variables correlating with the ordination as determined by *envfit* analysis are depicted with arrows.

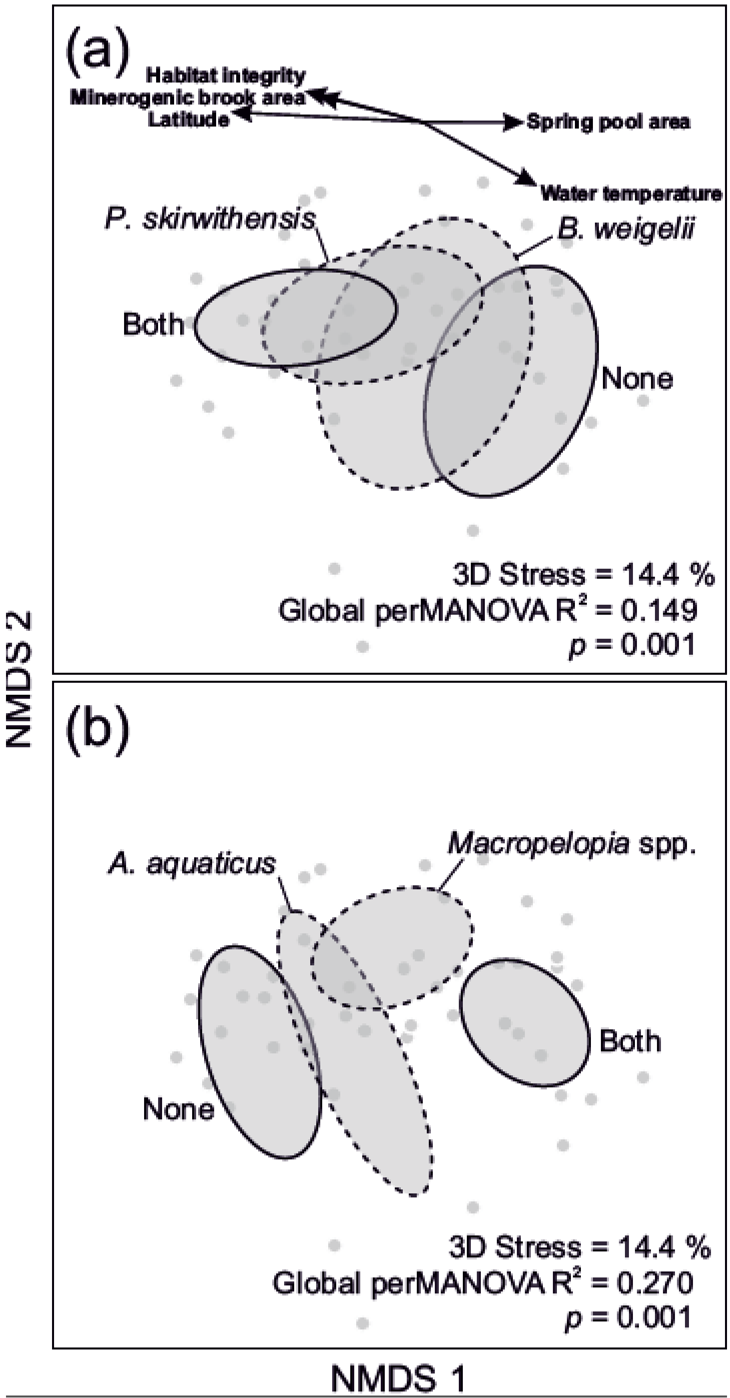
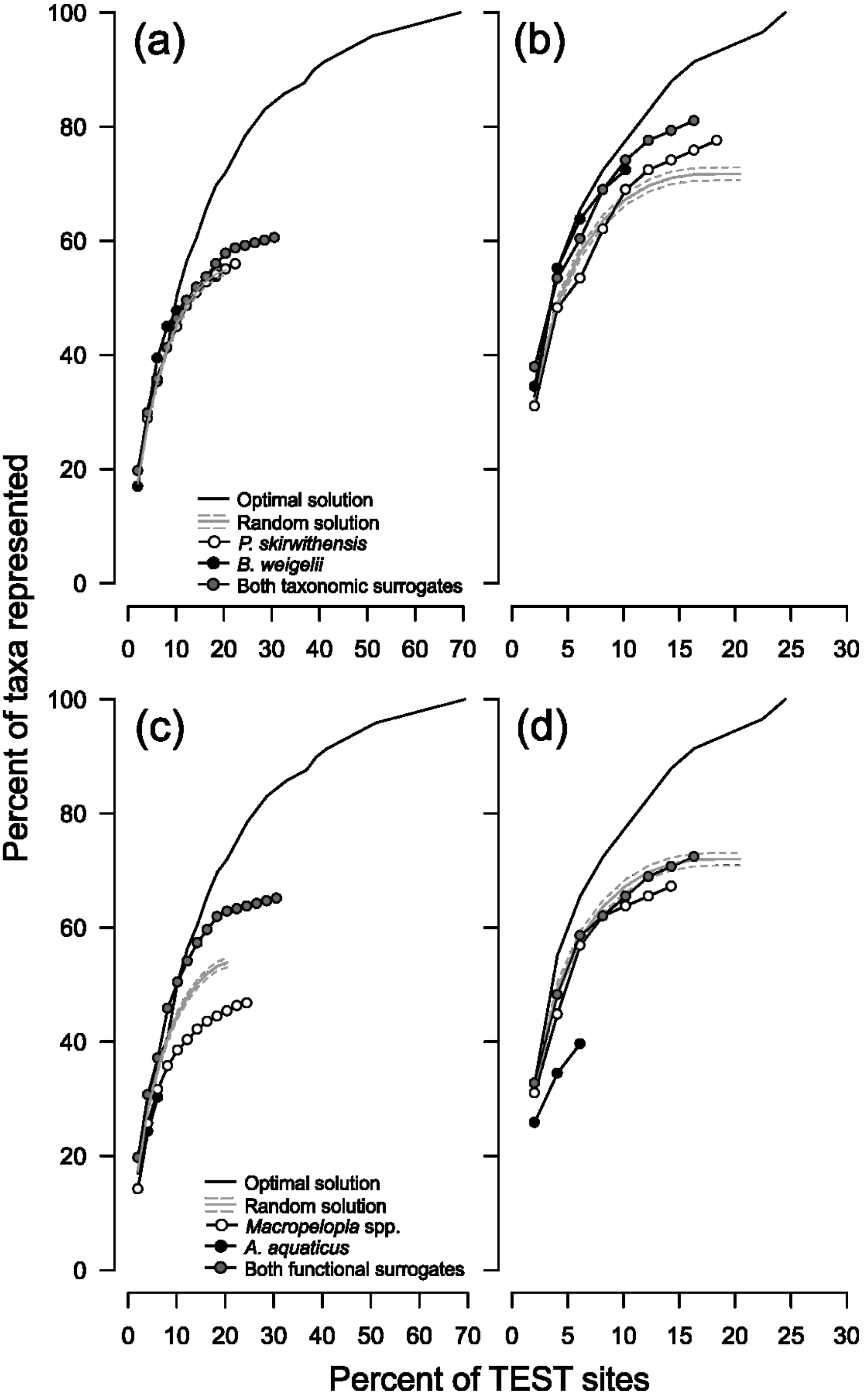


Figure 5. Cumulative percent of all taxa (a and c) and crenophilous taxa (b and d) represented under different site selection procedures based on a scoring algorithm (rarity-weighted richness), separately for taxonomic (a-b) and functional (c-d) surrogates. Dotted lines around the random solution denote ±95% confidence limits from 1000 randomizations.


(a)
(b)
(c)
(d)
Percent of taxa represented
Percent of TEST sites
0
20
40
60
80
100
0
10
20
30
40
50
60
70
0
5
10
15
20
25
30
Optimal solution
Random solution
P. skirwithensis
B. weigelii
Both taxonomic surrogates
Optimal solution
Random solution
Macropelopia spp.
A. aquaticus
Both functional surrogates