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Umbrella potential of plants and dragonflies for wetland conservation: a quantitative case study using the umbrella index

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Summary

1. Shortcuts to measuring biodiversity enable prioritization of conservation effort in the face of limited time, personnel and funding. The conservation umbrella approach focuses management effort according to individual species that may confer protection to a larger community. This approach can help guide the management agenda towards attainable goals by maximizing conservation returns per unit effort. The development of the umbrella index has shown promise in identifying umbrella species in terrestrial ecosystems but has received little attention with respect to the management of wetland ecosystems.

2. We used the umbrella index to assess the umbrella potential of vascular plants and dragonflies (Odonata) from 15 wetland impoundments in northern Mississippi, USA. The presence of adult odonates was determined by repeated visual surveys and plant lists were compiled from 50 plots per site.

3. Umbrella schemes, or the sites occupied by top umbrella species, missed large numbers of beneficiary species and occurrences. With one exception, umbrella schemes failed to optimize conservation returns relative to randomized schemes in both assemblages. Also, umbrella schemes approximately equalled the performance of non-umbrella schemes both overall and for species with a low rate of occurrence. Low occurrence rates in both assemblages may have hindered umbrella index performance because the index assumes that species with moderate occurrence rates have the most umbrella potential.

4. Cross-taxon analyses (Mantel tests and McNemar tests) suggested transferability of plant and dragonfly umbrella schemes, and non-random association between the plants and dragonflies in these wetlands.

5. *Synthesis and applications.* Despite the questionable performance of umbrella schemes in our study, the use of a quantitative ecological tool such as the umbrella index instead of political or popularity criteria is strongly recommended for future selection of umbrella species. The results of cross-taxon analyses supported growing evidence for spatial and functional relationships between wetland macrophytes and adult odonates. We suggest that the more easily measured assemblage can be used to set priorities for wetland conservation planning in circumstances where human resources are constrained.

Key-words: conservation, Odonata, umbrella index, umbrella potential, umbrella schemes, umbrella species, vascular plants, wetlands

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Introduction

Conservation planners contend with limited time, funding and personnel; thus they often rely on shortcuts for biodiversity measurement regarding reserve selection and prioritization of conservation efforts (Margules, Nicholls & Pressey 1988; Ryti 1992; Faith & Walker 1996;

Howard *et al.* 1998; Lawler *et al.* 2003; Kati *et al.* 2004). The umbrella species concept for biodiversity conservation allows managers to focus on a small number of species as proxies for protecting a larger community. Thus a reliable set of umbrella species can help managers allocate scarce resources to meet conservation objectives (Fleishman, Murphy & Brussard 2000). However, as with other surrogate concepts in conservation (Andersen *et al.* 2002; Sergio *et al.* 2006), umbrella species have been more a subject of scientific discourse than a proven tool for conservation action.

The selection of umbrella species is often subjective and based on non-ecological criteria, such as legal mandates or the species' charisma (Simberloff 1998; Rubinoff 2001). Ecological consideration is limited largely to range-based arguments (reviewed by Roberge & Angelstam 2004) and wide-ranging vertebrates have been popular candidates for umbrella species under the assumption that a landscape designed and managed to satisfy the most area-demanding species will also protect those species with lesser spatial requirements (Wilcox 1984; Beier 1993; Lambeck 1997; Fleishman, Murphy & Blair 2001b; Roberge & Angelstam 2004; Sergio *et al.* 2006). However, species that migrate over large areas may not be useful umbrellas if their population sizes are too small to maintain their own long-term viability (Berger 1997). Furthermore, indiscriminant protection of large tracts of land ignores variance in local species richness and may miss local hotspots of diversity (Prendergast *et al.* 1993; Fleishman, Murphy & Blair 2001b). It often is unrealistic to set aside and manage an entire landscape delineated by a large home range (Fleishman, Murphy & Blair 2001b). Recently, the traditional umbrella concept was generalized beyond area requirements to include any taxon whose conservation automatically confers protection to other naturally co-occurring taxa (Fleishman, Murphy & Brussard 2000; Roberge & Angelstam 2004).

Recognizing the need for objective, ecologically based selection of umbrella species, Fleishman, Murphy & Brussard (2000) developed the umbrella index (UI) to define, quantitatively, potential umbrella species. They demonstrated its utility on birds and butterflies (Fleishman, Murphy & Brussard 2000; Fleishman, Blair & Murphy 2001a; Betrus, Fleishman & Blair 2005). The umbrella index helps optimize the trade-off between available resources (e.g. financial) and the level of protection afforded to beneficiary species. The expectation is that managers will focus conservation actions according to umbrella schemes, which are the areas or sites supporting one or more potential umbrella species. For example, if a top umbrella species is found in 20 out of 25 sites in a planning area, then those 20 sites (80% effort) are where conservation actions should be focused. However, if 80% effort proves too costly, then a subset of these sites or umbrella species occupying fewer sites may be used. The goal is that umbrella-based site selection will balance levels of biodiversity protection with human resource limitations.

The umbrella index quantifies species' umbrella potential based on assumptions of co-occurrence, occurrence rate and sensitivity to human disturbance (Fleishman, Murphy & Brussard 2000; Fleishman, Murphy & Blair 2001b). First, a useful umbrella species must live with taxa that are to be protected. Secondly, umbrella species should have a moderate occurrence rate (e.g. 50% patch occupancy) within a given planning area. Candidate umbrella species with low occurrence rates may confer protection upon few other taxa. The drawbacks of focusing on widespread species include the impracticality of acquiring or managing vast expanses of land, as discussed above. Lastly, an umbrella species should be more sensitive to human disturbance than all or most co-occurring taxa. So two species could have the same mean co-occurrence and same occurrence rate but the species more sensitive to disturbance should offer a protection scheme with better potential to benefit at-risk species.

The umbrella species concept and the more quantitative umbrella index have received little attention with respect to wetland ecosystems and wetland taxa. Roberge & Angelstam (2004) reviewed 110 primary papers related to the umbrella concept and found only three related to wetland ecosystems (J.-M. Roberge, personal communication). Hess & King (2002) compiled expert judgements on potential surrogate species for conservation planning in an urbanizing region of North Carolina, USA, which included potential 'focal' species associated with riparian and bottomland forest. Other studies have approached the umbrella subject or similar surrogate concepts in aquatic ecosystems (Lawler *et al.* 2003; Hitt & Frissell 2004) but not in wetlands.

Research presented here used the umbrella index to select potential umbrella species of vascular plants and Odonata (damselflies, dragonflies) from wetlands. Wetlands often support a rich flora and have relatively high primary productivity (Mitsch & Gosselink 2000; Cronk & Fennessy 2001), thus plants make a natural choice for wetland conservation planning. Odonata are opportunistic predators whose large, colourful and charismatic adults draw empathy (Samways 1993; Primack, Kobori & Mori 2000; Hawking & New 2003) and whose larvae serve well in predicting diversity and structure of aquatic macroinvertebrate and vegetation assemblages (Briers & Biggs 2003; Foote & Hornung 2005). Odonata have been suggested as an umbrella taxon (Samways 1993; Hornung & Rice 2003) but no tests of their umbrella potential exist. We assessed the effectiveness of potential umbrella species both within and between wetland plants and odonates, and provide, as far as we are aware, the first test of the umbrella index in wetlands. Our study was largely a demonstration and performance evaluation of the approach rather than an attempt to provide actual umbrella species for broad use.

Materials and methods

STUDY SITES

The study was conducted in the warm-temperate East Gulf Coastal Plain region of the USA, an area of approximately 245 200 km^2 characterized by flat terrain and heavy amounts of rainfall. The study region was characterized by an altitudinal range of approximately 100–400 m and an average annual precipitation of 125–175 cm. The landscape included blackbelt chalk prairies, upland mixed deciduous and loblolly pine *Pinus taeda* L. forests and bottomland hardwood swamps. Land cover across the study region was approximately 31% agriculture, 17% low herbaceous vegetation (mix of unmanaged pasture, rural residential and natural or semi-natural grassland), 16% natural forest, 16% wetland, 15% agroforestry, 2% transportation, 2% non-wetland freshwater and 1% urban (Vilella *et al*. 2003).

We selected 15 wetland study sites among four study areas (three to four sites per study area) in northern and east-central Mississippi, USA. These sites comprised seven farm ponds (0·13–5·6 ha size range), four moist-soil managed marshes (1·8–11·1 ha), and four beaver *Castor canadensis* marshes (0·69–19·6 ha) (TerraServer-USA 2004). Three of the study areas were located within a 40-km radius (*c.* 5025 km^2 area) in north-east Mississippi (centred at 33·35°N, 88·90°W), approximately 165 km from the fourth area in extreme northern Mississippi (34·80°N, 89·45°W). Nearest-neighbour distances among study sites within these areas ranged from 170 m to 7·4 km (mean 1·8 ± 2·3 km). Immediate buffers (within 200 m of the wetland) varied from expanses of pasture or other open canopy habitat to herbaceous/forest mosaics or predominantly closed deciduous forest. Surrounding land use also varied among sites and included active or former cattle pasture, periodic mowing, controlled burning, selective timber management and tree plantations (Bried 2005).

VEGETATION SAMPLING

Vegetation was sampled once per site, with all 15 sites completed from May to August 2004. From a random starting point, 50 circular plots (0·5 m^2) were stratified throughout each wetland to include all major vegetation zones (e.g. floating-leaved, mixed emergent). All vascular plants in each plot were identified to species. Voucher specimens collected for most species were deposited in the Mississippi State University Herbarium. Further detail on the vegetation sampling methods employed is given in Ervin *et al*. (2006).

Smoothed plant species accumulations using Mao Tau moment-based rarefaction (Colwell, Mao & Chang 2004) were generated for the individual site with the greatest number of plant species in each wetland type. Completeness of sampling was estimated by dividing total observed species (S_{obs}) into expected asymptotic richness (S_{max}) based on the incidence coverage estimator (Lee & Chao 1994). This estimator performed the best overall on vegetation data sets and at small sample sizes in comparison with other estimators (Chazdon *et al*. 1998; J. T. Bried, unpublished data). The incidence-based coverage estimators were computed using the freeware EstimateS 7.5 (Colwell 2005).

ODONATA SAMPLING

We sampled adult dragonflies and damselflies on warm sunny days. The census of all study areas was completed within 4–6 consecutive days (sampling events) depending on weather, by the same observer. Each sampling event covered all sites within a single study area between 10:00 and 16:00, the local peak of odonate flight activity. The cycle was repeated for a total of eight sampling events per site from late May to mid-September 2004. Sites within study areas were surveyed in the same order (no rotation) across sampling events.

On each sampling event, the entire wetted area perimeter (0·16–0·92 km) of farm pond and moist-soil impoundments was walked slowly and continuously two to five times, depending on the site size. At the beaver marsh sites, major habitat zones were covered along a fixed transect route (*c.* 0·5 km). Surveys of each site lasted 1 h sampling $event^{-1}$. Across sampling events, more species were detected in the first 15 min (mean 10·9 ± 2·7 spp.) of survey than during the remaining 45 min (2·8 ± 1·7 spp.) combined (*t*-test, $P < 0{\cdot}0001$).

All encountered species of dragonfly and damselfly received an abundance score on a scale of 1–6 (1, 1–2 individuals observed; 2, 3–10; 3, 11–25; 4, 26–50; 5 ≥ 50; 6, the single clearly numerically dominant species). Species residency or attempted breeding was assumed when a species was detected on ≥ 3 sampling events with summed abundance scores of at least four and one or more reproductive behaviours (e.g. oviposition attempts, contact guarding, copulation wheels) recorded per event. Only these assumed resident species were analysed in the present study. Vouchers collected for most species were stored in the Mississippi Entomological Museum, Mississippi State University.

UMBRELLA INDEX

For every species, the umbrella index requires estimation of three parameters: co-occurrence, occurrence rate and sensitivity to human disturbance. Co-occurrence within plants and odonates was determined by computing proportions of the total resident species (all sites and sub sampling units combined) contained by each site. A species' mean co-occurrence equalled the sum of proportions over the sites containing that species divided by the total number of study sites, or 15, and ranged from 0 (occurs with few other species) to 1 (occurs with many other species). The degree of ubiquity was defined for each species as the departure from medium rarity, or by $1-2 \times |(N_{present}/N_{total}) - 0{\cdot}5|$, where N is the number of study sites. In this expression, departure

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from medium rarity is represented by subtracting one-half from the distribution ratio ($N_{present}/N_{total}$). Multiplication by 2 scales the output from 0 (ubiquitous or absent) to 1 (moderate occurrence rate).

Previous research with the umbrella index developed a multimetric index of disturbance sensitivity for birds and butterflies based on available life-history data (Fleishman, Murphy & Brussard 2000; Fleishman, Blair & Murphy 2001a; Betrus, Fleishman & Blair 2005). Such data were not available for every plant and odonate species we encountered, therefore a different approach was used to estimate disturbance sensitivity.

The 15 study sites spanned a gradient in human disturbance from mowed, trampled and polluted farm ponds to naturally occurring beaver marshes within protected natural areas. We qualitatively characterized this gradient using an anthropogenic activity index modified for Mississippi wetlands and based on the Minnesota wetland disturbance analysis (US EPA 2002; see Ervin *et al.* 2006 for modification details). Metric categories in this modified index included surrounding intensity of local land use (500 m radius), intactness and effectiveness of immediate buffer (50 m radius), hydrologic alteration, onsite habitat alteration and plant–water interspersion. Each metric category was scored on four levels of intensity (0, most disturbance; 3, least disturbance) and the sum of those integer scores yielded a composite site disturbance score from 0 (most disturbed) to 15 (least disturbed). These values were reversed from those used by Herman (2005), to yield the appropriate correlation with sensitivity to human disturbance. We then computed species indicator values (Dufrêne & Legendre 1997) to estimate the study site where a given species was most frequently observed and most abundant. To compute per species indicator values, a species' exclusiveness to a given site was multiplied by how often it was encountered across the site's subsample units (0·5-m^2 plots for plants, repeated surveys for odonates). We viewed these indicator values as surrogates for site preference, and each species was assigned the disturbance score of the site where its indicator value was highest. Relative species sensitivity was computed as the disturbance score for a given species divided by the maximum species disturbance score among the species recorded (i.e. one or more species that preferred the least disturbed site). As with the other two parameters, species sensitivity to human disturbance ranged from 0 (tolerant) to 1 (sensitive).

Values for co-occurrence, occurrence rate and disturbance sensitivity were summed to yield final umbrella index scores, from 0 for the lowest umbrella potential to 3 for the highest umbrella potential. We used the same arbitrary threshold for identifying potential umbrella species as used in previous studies (Fleishman, Murphy & Brussard 2000; Fleishman, Blair & Murphy 2001a), where the species must receive a score greater than the mean score plus 1 SD across all same-taxon species ($UI_{species\ score} > mean_{taxon\ score} + 1$ SD).

Several types of 'response currency' were summarized in relation to the umbrella schemes. We define umbrella schemes as the proportion and composition of sites supporting a given umbrella species. The response currencies are referred to as total occurrence, distribution ratio, partial protection and full protection. It might be helpful to visualize a site × species matrix where sites are row headings, species are column headings and cells contain a '1' to denote species presence in a given site. Total occurrence was measured as the sum of row totals or the sum of numbers of species in multiple sites in a given umbrella scheme. A distribution ratio was calculated per species as the column totals in an umbrella scheme divided by the actual number of sites where the species was found. Partial and full protection responses were expressed as proportions of the total species assemblage, where partial indicates those species protected in at least part of their range (species with a distribution ratio of > 0%) and full indicates those species protected in their full range (species with a distribution ratio of 100%) by a given umbrella scheme.

UMBRELLA SCHEME VS. RANDOM SCHEMES

As one performance test of the umbrella index within each assemblage, we asked whether umbrella schemes offered greater protection than random schemes. Total occurrence was used as the response currency for each level of effort (i.e. protecting 20%, 50% and 80% of sites); total occurrence in umbrella schemes at these effort levels became test statistics for comparisons against randomized schemes. Umbrella schemes consisted of the combination of sites with the highest ranked umbrella species or group of species.

Randomized schemes were the total possible combinations, or unique permutations, of study sites at the three levels of protection effort. The total possible k combinations of n sites is solved by $P_{k,n}/k!$, where $P_{k,n} = n!/(n–k)!$, and yields 455 possible three-site combinations, 6435 possible seven- or eight-site combinations, and 455 possible 12-site combinations of the total 15 wetland sites. The 'nchoosek' command in MATLAB 6·5 (MathWorks Inc., Natick Massachusetts) was used to list a set of occurrences for every possible site combination under each scheme. The occurrences in each possible combination were summed to determine how many combinations equalled or exceeded the test statistic, or the total occurrence of the umbrella scheme. Dividing this value by the number of possible combinations (k) gives a probability that may be interpreted in the same manner as P-values obtained from conventional hypothesis testing.

UMBRELLA SCHEME VS. NON-UMBRELLA SCHEMES

As an alternative performance test of the umbrella index, we asked whether umbrella schemes offered greater protection than non-umbrella schemes in terms of distribution ratio currency. Within each assemblage, we paired potential umbrella species with non-umbrella species ($UI_{species\ score} < mean_{taxon\ score} + 1$ SD) that occurred in the same number of sites. Comparing the umbrella scheme and non-umbrella scheme for the same set of species (all observed, within plants or odonates) meant the observations were paired.

Data violated normality in raw form and following transformation. A Monte Carlo simulation analogous to a paired *t*-test was run using the Resampling Stats (written by S. Blank, © 2005; Resampling Stats Inc., Arlington, Virginia) add-in for Excel. Observed distribution ratios were shuffled within rows 1000 times without replacement, and the difference between column means was re-calculated after each run. Shuffling within rows (i.e. within species) maintained the paired structure of observations. Statistical significance was approximated by how many of the randomly generated differences equalled or exceeded the observed difference (test statistic). This procedure was repeated for each paired umbrella and non-umbrella scheme in both assemblages. It was performed both for sets of total species and on sets of relatively narrow-range species only (those encountered in < 5 sites).

CROSS-TAXON UMBRELLA POTENTIAL

We followed Betrus, Fleishman & Blair (2005) and used McNemar's *Q*-test to examine whether wetland plants can serve as effective umbrellas for wetland odonates and vice versa. Our test compared total occurrence, partial protection and full protection measures between umbrella schemes from the same taxonomic group vs. cross-taxonomic umbrella schemes, each at 20%, *c.* 50%, and 80% effort.

Plant and odonate measures were organized in a 2 × 2 contingency table of umbrellas vs. beneficiaries. The McNemar test statistic (χ^2) was computed as the squared difference between same-taxon and cross-taxon response currencies (a, b) divided by their sum, or as $\chi^2 = (a - b)^2/(a + b)$. In all cases where $a + b > 20$, a continuity correction was added by down-weighting the numerator [$\chi^2 = (a - b)^2 - 1/(a + b)$] to improve the chi-square estimate of the exact binomial probability (Zar 1999; Sheskin 2000). In cases where $a + b \leq 20$, the binomial test for two proportions was used in place of the McNemar test.

Richness covariance and multivariate cross-taxon associations were tested via linear regressions and Mantel tests, respectively. The regression analysis is a standard check in these types of studies, but incidence patterns are more likely to correspond in different assemblages. The cross-taxon Mantel correlation for observed compositional similarity levels (Sørensen coefficient) among all pair combinations of sites was tested against 1000 randomized correlations using PopTools 2·6 for Excel (Hood 2005). In this way, the Mantel approach tested for non-random associations between taxa and provided an alternative direct assessment of cross-

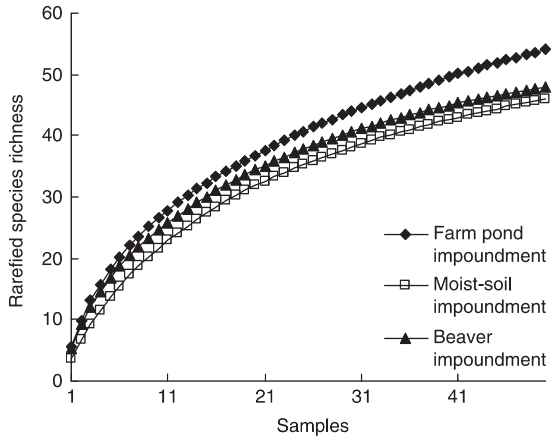

Fig. 1. Sample-based (0·5-m^2 circular plots) rarefaction curves of vascular plants at the site with the highest observed species accumulation in each of three wetland types. This interpolation used the moment-based estimator (Mao Tau) developed and recommended by Colwell, Mao & Chang (2004).

taxon umbrella potential (Su *et al.* 2004). Variables for regression and Mantel analyses included odonates, damselflies only, and dragonflies only vs. the full plant assemblage, the two most species-rich plant guilds (graminoids and forbs) and woody vegetation (combined shrubs, trees, woody vines).

Results

SPECIES RICHNESS

Totals of 157 plant species and 58 odonate species (20 damselflies, 38 dragonflies) were encountered. Estimated completeness of plant richness sampling was 83·5%, 66·5% and 79·3% ($S_{obs}/S_{max} \times 100$) for the most species-rich site among beaver, farm and moist-soil impoundments, respectively (Fig. 1). Based on the criteria for breeding attempts, frequency of detection and abundance, 41 odonate species (17 damselflies, 24 dragonflies) were retained as probable or possible resident species. No new odonate species were added beyond the first six sampling events at any site or even beyond the first four sampling events at 12 sites.

UMBRELLA INDEX

Umbrella index scores of 25 plant species fell above the arbitrary cut-off (1·223) for umbrella potential (Table 1), and each of the four top-ranked species occurred in eight sites. Distribution of the first-ranked plant umbrella species, the grass *Leersia oryzoides* (L.) Sw., overlapped with 52% of total plant occurrence. The second-ranked plant umbrella, *Polygonum densiflorum* Meisn., occurred in four sites where the first-ranked species was not found, making an umbrella scheme where effort (80%) nearly equalled the additive total occurrence (79%). Plant umbrella scheme saturation (100% site representation) was reached after inclusion of the next seven potential umbrella species.

Table 1. Ranked umbrella index (UI) scores, additive proportion of wetland sites containing top umbrella species (Effort) and additive response currency

Top umbrella species*	UI score	Effort (%)	Cumulative response (%)†		
			TO	PR	FR
Plants					
Leersia oryzoides	2·076	53	52	80	21
Polygonum densiflorum	2·003	80	79	90	45
Mikania scandens	2·003	87	85	93	62
Juncus elliottii	1·994	93	92	97	71
Four species	1·863–1·886	Same	Same	Same	Same
Rubus argutus	1·787	100	100	100	100
Sixteen species	1·569–1·780	Same	Same	Same	Same
Odonata					
Enallagma geminatum	2·271	47	49	85	20
Libellula cyanea	2·002	67	70	93	29
Lestes inaequalis	1·995	73	78	95	42
Libellula vibrans	1·844	80	84	95	59
Anax junius	1·816	80	Same	Same	Same
Nehalennia integricollis	1·808	80	Same	Same	Same

*$UI_{species\ score} > mean_{taxon\ score} + 1$ SD; $mean_{plants} = 1{\cdot}223 \pm 0{\cdot}342$; $mean_{odonates} = 1{\cdot}376 \pm 0{\cdot}367$.
†TO, total occurrences (the total incidence of all species in a given umbrella scheme); PR, partial range (proportion of species where a given umbrella scheme intercepts > 0% distribution); FR, full range (proportion of species where a given umbrella scheme intercepts 100% distribution).

Table 2. Proportion of all possible wetland site combinations with response currency (total occurrences) equal to or exceeding that of given umbrella schemes. The three-site umbrella schemes of both taxa included those sites containing the most potential umbrella species, whereas the other two umbrella schemes were pulled from Table 1

Umbrella scheme	Test statistic*	No. ≥ test statistic†	*P*-value
Plants			
3 sites (20% effort)	122	35	35/455 = 0·075
8 sites (*c.* 50% effort)	284	4680	4680/6435 = 0·727
12 sites (80% effort)	428	369	369/455 = 0·809
Odonata			
3 sites (20% effort)	52	162	162/455 = 0·356
7 sites (*c.* 50% effort)	121	1258	1258/6435 = 0·196
12 sites (80% effort)	210	3	3/455 = 0·007

*Total occurrences.
†Number of possible permutations where total occurrences equalled or exceeded the test statistic.

Six odonate species scored above the cut-off value (1·376) for umbrella potential (Table 1). Distribution of the top-ranked umbrella species, the damselfly *Enallagma geminatum* (Kellicott), overlapped with 49% of total odonate occurrence. Overall in both taxa, increasing levels of effort matched proportional accumulation of total occurrence (Table 1), making it unlikely that the umbrella index found an optimum solution. The proportion of species protected across part vs. all of their range was similar between plant and odonate umbrella schemes. The 80% effort umbrella schemes missed 10% of beneficiary plant species and 5% of beneficiary odonate species, based on partial range.

UMBRELLA SCHEME VS. RANDOM SCHEMES

Umbrella schemes showed mixed success relative to random schemes at containing the optimum total occurrence levels (Table 2). In plants, only 7·5% of the possible 455 three-site combinations covered as much or more total occurrence than the three-site umbrella scheme. The 12-site odonate umbrella scheme picked up the optimal total occurrence, which meant more total occurrence than all 455 possible 12-site combinations, except for three ties (Table 2). Total occurrence levels under umbrella schemes for the remaining cases, however, were far below optimal.

UMBRELLA SCHEME VS. NON-UMBRELLA SCHEMES

For plants, the mean distribution ratio in umbrella schemes was higher than that in non-umbrella schemes for 71% of available test comparisons (17 pairs) but only one case yielded a significant difference after conservative Bonferroni adjustments (permutation *t*-test, $n = 157$ species, $P = 0{\cdot}006$). Only one significant difference was found in 10 available comparisons for odonates ($n = 41$ species, $P = 0{\cdot}017$) and the non-umbrella scheme showed the higher mean distribution ratio in this case. In both assemblages, the same conclusions were reached from analyses run only on beneficiaries with low occurrence rate, defined as species encountered in < 5 sites. There was no rank association between disturbance sensitivity and rarity (1 – distribution ratio) in the plants (Spearman's $r_s = 0{\cdot}049$, $P = 0{\cdot}543$) or odonates ($r_s = 0{\cdot}125$, $P = 0{\cdot}436$). As with total occurrence, it did not appear that umbrella schemes maximized the currency of distribution ratio, whether overall or for potentially rare species.

CROSS-TAXON UMBRELLA POTENTIAL

McNemar tests indicated two significant differences between protection levels of same- vs. cross-taxonomic umbrella schemes (Table 3). The power of the statistical tests was low, but group differences were small (e.g. 0·17 unit maximum difference in 18 test cases). In six cases, including one of the significant differences, the cross-taxon umbrella scheme offered more protection than the same-taxon umbrella scheme. Non-random patterns of cross-taxon association were suggested by multivariate correlations (Table 4), yet all cross-taxon patterns of species richness for the same set of variables were non-linear (all $r^2 \leq 0{\cdot}13$, all $P \geq 0{\cdot}179$).

Discussion

The umbrella index brings an objective, ecologically based approach to identifying potential umbrella species, and has clear applications for reserve selection in conservation planning. It tries to reconcile concerns with the traditional umbrella species concept by balancing

Table 3. Proportions of total occurrences, partial ranges and full ranges of beneficiaries protected by same-taxon (U_{same}) vs. cross-taxon (U_{cross}) umbrella schemes

	Total occurrences		Partial range		Full range	
Umbrella scheme	U_{same}	U_{cross}	U_{same}	U_{cross}	U_{same}	U_{cross}
Plants						
3 sites (20% effort)	0·23	0·19	0·50	0·42	0·05*	0·12*
8 sites (*c.* 50% effort)	0·52*	0·43*	0·80	0·72	0·21	0·19
12 sites (80% effort)	0·79	0·79	0·92	0·90	0·45	0·49
Odonata						
3 sites (20% effort)	0·21	0·22	0·61	0·68	0·10	0·05
7 sites (*c.* 50% effort)	0·49	0·57	0·85	0·93	0·20	0·20
12 sites (80% effort)	0·84	0·83	0·95	0·93	0·59	0·42

*$0·025 < P \leq 0·05$; statistical differences based on McNemar tests or, when $n < 20$, binomial proportion tests comparing U_{same} with U_{cross}.

area demands with protection of species likely to have greater conservation needs, such as rare or disturbance-sensitive species. Furthermore, umbrella schemes are meant to balance protection of numerous species and high proportions of their distributions with a feasible amount of site or landscape protection. This built-in combination of features distinguishes the umbrella index from integer-programming, simulated annealing and other complementarity algorithms used to locate optimum site networks based strictly on the amount of species representation (Rodrigues & Gaston 2002). A quantitative and ecologically valid tool such as the umbrella index should supersede the use of political or popularity criteria for any selection of umbrella species in the future.

Protection levels offered by an umbrella scheme should exceed units of conservation effort, such as the proportion of sites included in a conservation network. The protection levels suggested here roughly matched rather than exceeded the effort (Table 1). Other quantitative umbrella studies reported relatively high or near-optimal protection levels (Howard *et al.* 1998; Fleishman, Murphy & Brussard 2000; Fleishman, Blair & Murphy 2001a; Lawler *et al.* 2003; Sergio *et al.* 2006), whereas our comparisons with random and non-umbrella schemes demonstrated the lack of optimal solutions (e.g. Table 2). Andelman & Fagan (2000) reported that surrogate schemes based on umbrella species performed worse than or equivalent to random schemes in terms of total species protection. However, they tested umbrella species with occurrence rates as low as 5% and it was not clear whether response currencies were compared with random schemes of equal size. Although the current study suggests umbrella schemes were below optimal, this does not automatically mean the index is flawed, because some assemblages simply may not offer species that meet index criteria in certain situations. Moreover, the index is balancing amount of protection with feasibility and conservation priority (e.g. commitment to disturbance-sensitive taxa) and therefore umbrella schemes should not be expected to always cover the maximum species richness or incidence.

In our study, more than 80% of plant species and nearly 60% of odonate species were found in five or fewer sites. A preponderance of rarity (i.e. low occurrence rate) may have interfered with umbrella species selection by limiting co-occurrence. For example, three of the seven site-exclusive odonates were missed by the top odonate umbrella scheme and 24 of the 47 site-exclusive plants were missed by the top plant umbrella scheme. This impeded all response currencies and automatically took partial or full protection away from 27 potential beneficiaries. Only 17% of the detected species in each assemblage were found in 6–10 sites, meaning relatively few species met the ideal occurrence rate (moderate) assumed by the index.

The rare species (< 5 sites) distribution ratio, defined as the proportion of a species' distribution overlapped by an umbrella scheme, was not covered any differently by umbrella schemes than distribution ratios of all species considered at once. This is not surprising given co-occurrence limitations from low occupancy rates and the potential for rare-species exclusion from otherwise encouraging umbrella schemes. For example, Lawler *et al.* (2003) found that site selection schemes based on six indicator taxa included 61–82% of possible beneficiaries in the mid-Atlantic USA but most of the rare and at-risk species were excluded.

The variation in perceived disturbance or flaws with our disturbance sensitivity index may have further weakened selections by the umbrella index. Disturbance ranged from cattle trampling and low water clarity in farm ponds to intensive hydrologic alteration (e.g. annual drainage, levees) and disking in moist-soil impoundments, and well-vegetated beaver ponds in forested surroundings. Disturbance scores for these sites ranged from 3 to 13 out of a possible range of 0–15 available in the anthropogenic activity index. The

Table 4. Multivariate cross-taxon correlations (r, standardized Mantel statistic) from Mantel tests

	All plants		Graminoids		Forbs		Woody	
	r	P	r	P	r	P	r	P
Odonata	0·438	< 0·001*	0·368	0·003*	0·404	< 0·001*	0·189	0·078
Damselflies	0·480	< 0·001*	0·399	0·002*	0·429	< 0·001*	0·211	0·075
Dragonflies	0·148	0·072	0·123	0·129	0·163	0·071	0·079	0·218

*Significance respective to the conservative Bonferroni-corrected error rate ($\alpha = 0·05 \div 12 = 0·0042$).

mix of habitat types and disturbance regimes, and the variable distances among sites, probably contributed to wide richness and compositional variation among sites, and consequently to reduced co-occurrence. Conversely, sample units in Fleishman, Blair & Murphy (2001a) ranged from biological reserves to golf courses and housing projects, yet they reported high response currencies for same-taxon umbrella schemes. Their research was conducted over a larger spatial extent than here, but apparently study systems with heterogeneous disturbance may still draw strong response currencies from umbrella conservation schemes; multiscale evaluations might elucidate causes of inconsistency in umbrella index performance.

Disturbance sensitivity values hinged on the assumption that close links to site conditions are reflected in high abundance and frequency, as represented by species' indicator scores. At best, those quantities were rough proxies for site preference, but they were the only quantitative data available for assignment of species sensitivity.

Linear correlations between macrophytes and adult odonates were absent or weak in this study and elsewhere (Sahlen & Ekestubbe 2001; Hornung & Rice 2003). Differential resource limitations (e.g. prey abundance, fire regimes) and scale dependence (Wiens 1989) among species make it unlikely that species number will co-vary in a linear pattern across taxa. Consequently, the use of species identity and complementarity instead of richness to represent relationships across taxa is widely recommended for coarse-filter conservation (Howard *et al*. 1998; Oliver, Beatie & York 1998; Kotze & Samways 1999; Vessby *et al*. 2002; Grand *et al*. 2004; Su *et al*. 2004; Anand, Laurence & Rayfield 2005).

The similarity in protection levels offered between same- vs. cross-taxon umbrella schemes was encouraging, and supports the dependence of odonates on vegetation for structure, oviposition sites, resting and emergence platforms and territorial activity (Buchwald 1992; Steytler & Samways 1995; Clark & Samways 1996; Stewart & Samways 1998; Corbet 1999; Gibbons, Reed & Chew 2002; Foote & Hornung 2005). Our results echoed those of Betrus, Fleishman & Blair (2005), who found only two significant differences in 32 McNemar test comparisons of same- vs. cross-taxonomic umbrella schemes for birds and butterflies. In the current study, there also were significant Mantel correlations of the damselfly and Odonata assemblages with the full plant assemblage and groupings of plants into life-form guilds. As relatively weak fliers, damselflies generally perch more frequently than dragonflies and may have a greater need for protective cover, plus almost all known damselfly species lay eggs inside plant tissue (Corbet 1999). Growing evidence for spatial and functional associations between wetland plants and odonates suggests that wetland managers may be able to choose one or the other for adequate conservation planning in resource-limited situations. Even when different subsets of species within taxa inhabit different types of wetlands, as they did here, cross-taxonomic associations within those wetland types may hold, at least under certain spatial scales or landscape context.

Maintenance of characteristic wetland plant associations helps promote healthy dragonfly assemblages, and the ecological requirements of dragonflies may be used to help protect wetland plants. For example, conservation actions based on ecological requirements of odonates (Purse *et al*. 2003), such as delineating natural buffers around wetlands according to dragonfly spatial dynamics (Bried & Ervin 2006), might insulate wetland vegetation and in turn increase habitat quality for odonates and other wetland fauna. Fortunately, adult stages of Odonata are easy to sample and use as conservation umbrellas relative to most other wetland invertebrates. This is important given that vertebrate-based umbrella schemes can be ineffective for invertebrate conservation (Oliver, Beatie & York 1998; Rubinoff 2001) and that conservation actions based solely on terrestrial taxa may not encompass the needs of aquatic and wetland species (Lawler *et al*. 2003).

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