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Contributed Paper

Defining and Evaluating the Umbrella Species Concept for Conserving and Restoring Landscape Connectivity

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Abstract: *Conserving or restoring landscape connectivity between patches of breeding habitat is a common strategy to protect threatened species from habitat fragmentation. By managing connectivity for some species, usually charismatic vertebrates, it is often assumed that these species will serve as conservation umbrellas for other species. We tested this assumption by developing a quantitative method to measure overlap in dispersal habitat of 3 threatened species—a bird (the umbrella), a butterfly, and a frog—inhabiting the same fragmented landscape. Dispersal habitat was determined with Circuitscape, which was parameterized with movement data collected for each species. Despite differences in natural history and breeding habitat, we found substantial overlap in the spatial distributions of areas important for dispersal of this suite of taxa. However, the intuitive umbrella species (the bird) did not have the highest overlap with other species in terms of the areas that supported connectivity. Nevertheless, we contend that when there are no irreconcilable differences between the dispersal habitats of species that cohabitate on the landscape, managing for umbrella species can help conserve or restore connectivity simultaneously for multiple threatened species with different habitat requirements.*

Keywords: circuit theory, corridor, dispersal, landscape connectivity, modeling, surrogate species

Definición y Evaluación del Concepto de Especie Paraguas para Conservar y Restaurar la Conectividad de Paisajes

Resumen: *Conservar o restaurar la conectividad de paisajes entre fragmentos de hábitats de reproducción es una estrategia común para proteger a las especies amenazadas de la fragmentación de hábitat. Al manejar la conectividad para algunas especies, generalmente vertebrados carismáticos, se asume comúnmente que estas especies servirán como paraguas de conservación para otras especies. Probamos esta suposición desarrollando un método cuantitativo para medir el traslape en la dispersión de hábitat de tres especies amenazadas que habitan en el mismo paisaje fragmentado: un ave (el paraguas), una mariposa y una rana. La dispersión de hábitat se determinó con Circuitscape, al cual se le establecieron parámetros con movimientos de datos colectados para cada especie. Pese a las diferencias en la historia natural y el hábitat de reproducción, encontramos un traslape sustancial en las distribuciones espaciales de áreas importantes para la dispersión de este conjunto de taxones. Sin embargo, la especie paraguas intuitiva (el ave) no tuvo el traslape mayor con otras especies en términos de áreas que apoyen la conectividad. A pesar de todo, sostenemos que cuando no hay diferencias irreconciliables entre la dispersión de hábitats de las especies que cohabitan en el paisaje, manejar*

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todo para la especie paraguas puede ayudar a conservar o restaurar simultáneamente la conectividad para múltiples especies amenazadas con requerimientos de hábitat diferentes.

Palabras Clave: conectividad de paisajes, corredor, dispersión, especies sustitutas, modelado, teoría de circuitos

Introduction

Habitat loss and fragmentation are the most important threats facing endangered species (Wilcove et al. 1998). One strategy used to overcome the negative effects of habitat fragmentation is to conserve or restore landscape connectivity through, for example, the creation of landscape corridors (Crooks & Sanjayan 2006; Hilty et al. 2006). Increased landscape connectivity enhances dispersal frequency (Haddad et al. 2003; Gilbert-Norton et al. 2010), population persistence (Gonzalez et al. 1998), and species diversity (Damschen et al. 2006). Yet, restoring connectivity across large landscapes for multiple animals and plants can be challenging because species that differ in habitat, body size, dispersal ability, or lifespan (among other traits) may require connectivity at different scales or in different designs. In practice, connectivity is often restored for one or a few focal species, typically a large mammal or other charismatic vertebrate with a large home range or potential for dispersal. An often untested assumption is that this focal species will provide a connectivity umbrella for other less charismatic species. Here, we defined the umbrella species concept for connectivity, established null criteria against which to evaluate the concept, and tested the concept with detailed dispersal data for a taxonomically diverse group of rare, sympatric species.

Most conservation biologists are familiar with the umbrella species concept, at least as it applies to the conservation of primary habitats, such as breeding or foraging sites. Under the classic definition of the umbrella concept (Caro 2010), conservation of sufficient habitat for an animal with a very large home range should require areas so large that they also provide sufficient area for most species with smaller home ranges (Andelman & Fagan 2000). In practice, studies that identify umbrella species (Fleishman et al. 2000; Roberge & Angelstam 2004) attempt to find a single species, or a small set of species, whose needs can be used to guide management for a larger group of species for which there is less information. For example, the Northern Spotted Owl (*Strix occidentalis caurina*), a species that needs large forested areas for its territories, has been considered an umbrella for other species, including mollusks and salamanders, in old-growth forests of the Pacific Northwest, U.S.A. (Dunk et al. 2006). The umbrella species concept differs from the broader concept of an indicator species in that umbrella species are selected to represent particular populations or species instead of overall biodiversity, and the scale of analysis is generally local rather than regional (Caro 2010). Generally, umbrella species have been identified based on rarity (Niemi et al. 1997) or patterns of cooccurrence (Fleishman et al. 2000).

Identifying effective connectivity umbrella species can be more challenging than identifying umbrella species for the conservation of primary habitats for several reasons. First, whereas under the traditional definition of umbrella species breeding and foraging habitats were the primary focus, a good connectivity umbrella must also represent habitats that facilitate dispersal of a suite of other species, and environments that facilitate dispersal may be quite different from those that are suitable for breeding or foraging (Haddad & Tewksbury 2005; Kuefler et al. 2010). Differences in dispersal distances, sensitivity to barriers, and other aspects of dispersal biology can prevent a species from serving as an effective connectivity umbrella even if its breeding or foraging habitat overlaps with or encompasses those of other species of concern. Second, movement behaviors are complex and dispersal events are difficult to observe directly (Turchin 1998). Most efforts to incorporate connectivity into conservation planning draw on expert opinion to determine dispersal habitat (Beier et al. 2008; 2009; Cushman et al. 2013; but see Cushman & Landguth 2012). In practice there may often be few alternatives, but expert opinion tends to rely on circular logic: dispersal habitat is either equated with breeding habitat or determined from where animals are observed. Yet, because animals often move quickly through nonbreeding habitat (Kuefler et al. 2010), they are less likely to be observed in dispersal habitat.

We define a good connectivity umbrella as a species for which conservation or restoration of its dispersal habitat also facilitates dispersal of other target species (Fig. 1). This is a case of management synergy (Fig. 1b) in which managing connectivity for one species also benefits other nontarget species. The umbrella species concept has been previously extended to address connectivity (Roberge & Angelstam 2004; Beier et al. 2009; Cushman & Landguth 2012; Cushman et al. 2013), but this work often assumed management synergy and did not directly address the possibility that managing dispersal needs of cooccurring species can be zero sum or less than zero sum (i.e., the conservation or restoration of connectivity for one species may have no benefit [independence, Fig. 1c] or may even retard dispersal of other species [conflict, Fig. 1d]). These conflicts can emerge when environments that are permeable for one species are relatively impermeable to others and when the spatial distribution of these habitats are interspersed.

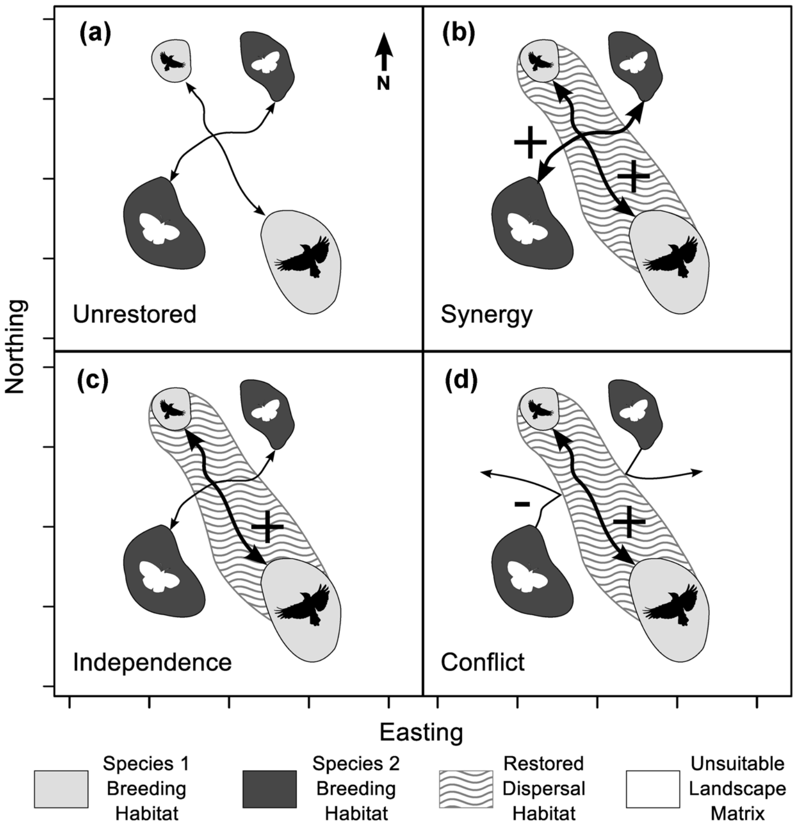

Figure 1. Illustration of the application of the connectivity umbrella concept to 2 species in an area where (a) connectivity between habitat patches has not been restored or protected (arrows, dispersal; thickness of arrows and lines proportional to the amount of dispersal), (b) restoration or protection of dispersal habitat for species 1 enhances dispersal of species 2, making the species umbrellas for each other and providing opportunities for management synergy, (c) restoration or protection of dispersal habitat for species 1 neither enhances nor impedes dispersal of species 2 allowing the 2 species to be managed independently, and (d) restoration or protection of dispersal habitat for species 1 impedes dispersal of species 2 creating a potential for management conflict.

In this work, we developed a quantitative framework for measuring the effectiveness of a connectivity umbrella species. We then used this framework and field-validated dispersal models to assess whether synergies exist in connectivity management for a suite of rare taxa in a fragmented landscape. Our candidate umbrella species was the federally endangered Red-cockaded Woodpecker (*Picoides borealis*), a major target for habitat conservation and restoration in the longleaf pine (*Pinus palustris*) ecosystem of the southeastern United States (Wilcove & Lee 2004). We also selected for study 2 other rare animals, the federally endangered St. Francis' satyr butterfly (*Neonympha mitchellii francisci*) and the Carolina gopher frog (*Rana capito capito*), designated by the state of North Carolina as threatened. We selected this suite of focal species a priori to have divergent habitat requirements and dispersal behaviors, with the aim to provide a stress test for multispecies connectivity management.

Methods

We mapped important breeding and dispersal habitats for each focal species in our study area; developed species-specific estimates of resistance to dispersal (the degree to which a particular habitat limits movement) for each type of habitat based on detailed behavioral data; modeled spatial patterns of dispersal for each species; and determined their umbrella effectiveness by analyzing the spatial overlap of dispersal areas for all 3 species.

Study Area

Our study area encompassed the landscape in and around 2 U.S. Army installations located in the Sandhills Ecoregion of North Carolina in the southeastern United States: the approximately 62,000 ha Fort Bragg and the nearby approximately 3000 ha Camp MacKall. We also included lands in a rectangular region extending 5 km beyond the borders of both installations, including private lands as well as those managed by The Nature Conservancy, the North Carolina Division of Parks and Recreation and the North Carolina Wildlife Resources Commission (Fig. 2a). These managed lands consist of longleaf pine forest, riparian habitats, and open areas, many of which have been subjected to frequent (2- to 5-year interval) prescribed fire. The landscape outside these managed lands is a mix of urban, agricultural, and forested areas where fire is suppressed. Regular fire is critical for many endemic species in this landscape (Van Lear et al. 2005), and restoration of the longleaf pine ecosystem is focused on the reintroduction of regular fire.

Study Species and Input Data

For our 3 study species, Red-cockaded Woodpeckers, St. Francis' satyr butterflies, and Carolina gopher frogs,

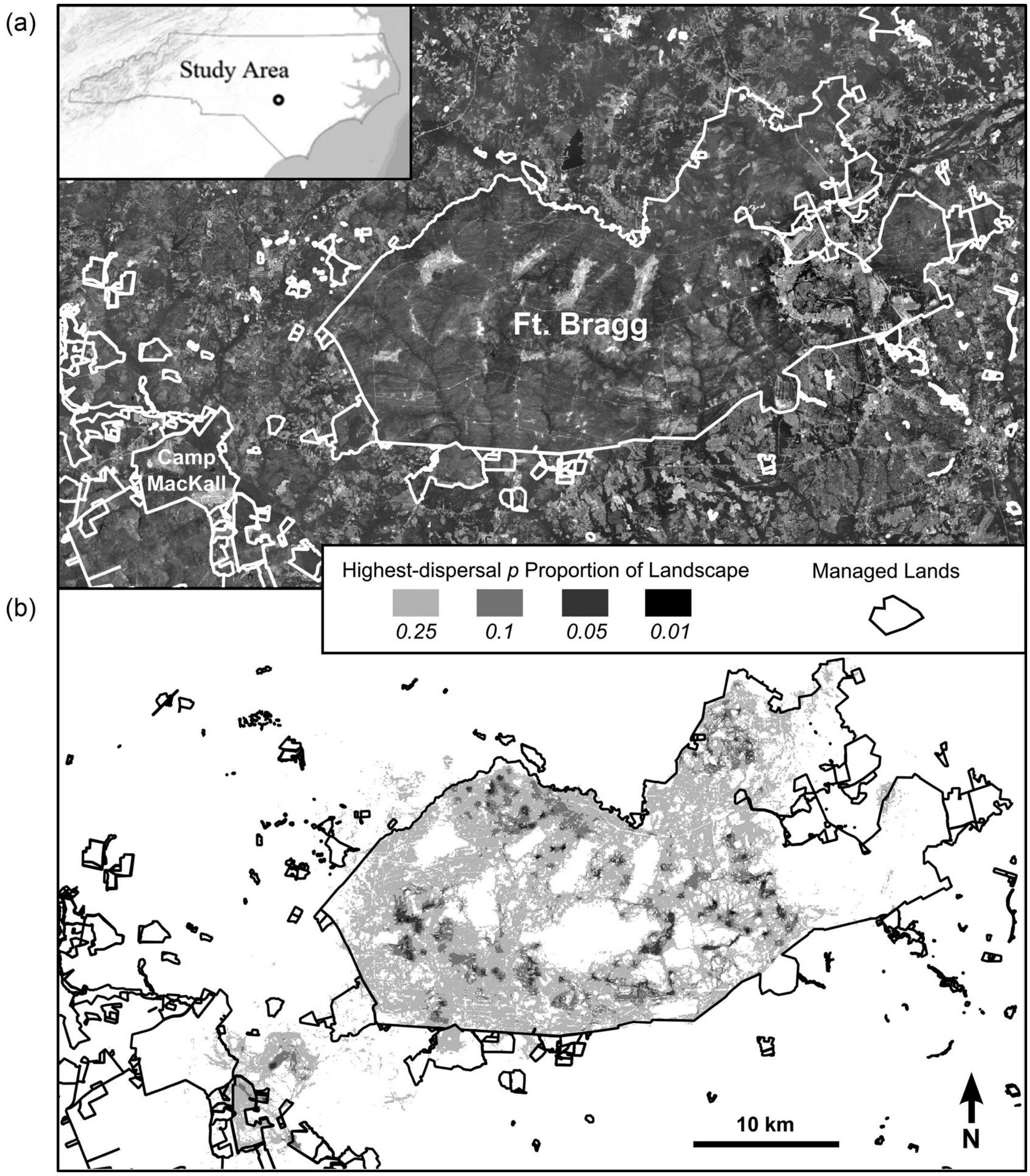

Figure 2. Maps of the study area in North Carolina (U.S.A.) and important dispersal areas for 3 threatened species (Red-cockaded Woodpecker, Carolina gopher frog, and St. Francis satyr butterfly): (a) 2008 U.S. Geological Survey aerial photograph showing the outlines of the military installations of Ft. Bragg and Camp MacKall and other properties actively managed for wildlife and (b) areas of spatial overlap of dispersal for all 3 species at several thresholds of dispersal density with the threshold representing the 0.25, 0.1, 0.05, and 0.01 proportion of the landscape with the highest relative dispersal frequency. To conceal the locations of active breeding sites for endangered species, the map in (b) shows a dispersal model scenario that includes both currently occupied and potential breeding habitats (see Supporting Information).

lack of connectivity was previously identified as a potential threat to their long-term persistence (U.S. Fish and Wildlife Service 2003; Kuefler et al. 2008; Roznik et al. 2009). We delineated the locations of current breeding habitats for each species and created resistance maps representing the degree to which each area of intervening habitat impeded dispersal between those breeding habitats (Adriaensen et al. 2003). These methods have been described in detail elsewhere (Fields 2012; Hudgens et al. 2012; Trainor et al. 2013); we briefly review details relevant to our study.

Our study area harbors the largest extant population of Red-cockaded Woodpeckers species. Dispersal of juvenile female Red-cockaded Woodpeckers between breeding territories has a large influence on population viability (Schiegg et al. 2006). Breeding habitats in this species are restricted to mature longleaf pine forests (Conner et al. 2001; Rudolph et al. 2002; Walters et al. 2002), and we knew the locations of all active and recently active breeding territories in this landscape circa 2008 ($n = 564$). Previous analysis showed that dispersing juvenile females of this species perform extensive searches for breeding habitat prior to their final dispersal to a new breeding territory (Kesler et al. 2010) and will disperse through most forested habitats but avoid open areas (Kesler & Walters 2012).

We used standard radio-telemetry techniques (detailed in Trainor et al. 2013) to monitor predispersal (prospecting) movements for 34 juvenile female birds during 2006 and 2007 at Ft. Bragg. During each 4-h monitoring session, we located each individual at least twice per hour and recorded the bird's GPS location. We assessed the landscape resistance to prospecting movement in a generalized linear mixed modeling framework (Zeller et al. 2014) by comparing Landsat- and lidar-derived attributes (Supporting Information) of each location used by each bird while prospecting with 2 randomly selected locations in the prospecting range of each individual. We used model-averaging based on Akaike weights (Burnham & Anderson 2002) to estimate the optimal resistance surface. To validate this resistance surface, we assessed its ability to predict an independent data set of observed juvenile female dispersal events from 2005 ($n = 57$) and 2006 ($n = 39$). Specifically, we compared the cumulative least-cost-path distance between pairs of territories that received different numbers of prospecting visits in a discrete-choice model. Details of the model fitting and performance evaluation are in Trainor et al. (2013).

St. Francis' satyr is known to occur only at Ft. Bragg. Its populations are found in beaver-maintained wetland meadows along small streams (Kuefler et al. 2008). Because habitat is constantly shifting, this butterfly has a metapopulation structure, so persistence on the landscape depends on dispersal between transient habitat patches (Kuefler et al. 2010; Milko et al. 2012). We used long-term monitoring records (summarized in Kuefler et al. 2008) to determine all known breeding locations for this species.

We collected data on movement paths of naturally occurring and experimentally released animals in all common habitat types and at boundaries between habitats on Ft. Bragg in 2006 and 2007 (details in Kuefler et al. 2010). For each habitat type, we calculated the probability that a butterfly would enter the habitat by monitoring movement of individuals released at boundaries between habitat types ($n = 59$ individuals). Using a correlated random walk model, we estimated habitat-specific mean displacement rate from independent observations of butterflies ($n = 25$) released in continuous blocks of habitat and from naturally occurring individuals ($n = 29$) (Kareiva & Shigesada 1983). We combined entry probability and mean displacement rate to estimate the resistance of each habitat to dispersal (Supporting Information). Movement data for St. Francis' satyr were collected for naturally occurring individuals in breeding habitat only. In light of St. Francis' satyr's endangered status, we used the similar species Appalachian brown (*Satyrodes appalachia*) as a surrogate for release experiments and to collect movement data in low-quality habitats. Hudgens et al. (2012) validated this surrogate species approach by comparing movement and boundary-crossing behaviors of the 2 species in wetland environments. They found that distributions of turn angles and boundary-crossing behaviors did not differ between species.

Carolina gopher frogs, a North Carolina threatened species, must migrate seasonally between breeding habitats (fish-free upland ponds [Beane et al. 2010]) and nonbreeding habitats (upland forests). We mapped all known breeding ponds in our landscape through field surveys and tracked individuals by marking them with florescent dye powder as they left natural breeding ponds or artificially created breeding ponds that we located at habitat boundaries. We derived resistance values for this species with techniques identical to those we used for butterflies (Supporting Information). Because of low numbers of Carolina gopher frogs encountered during the field study ($n = 5$), our movement data included paths of both this species and those of ornate chorus frogs (*Pseudacris ornata*) ($n = 29$), a more common species that shares breeding habitats with Carolina gopher frogs. A more detailed description of the study design and movement data collected for this species can be found in Fields (2012).

Assessing Landscape Connectivity

To assess the spatial distribution of connectivity for each species, we created dispersal models based on circuit theory as implemented in the Circuitscape software (Version 3.5.4, McRae et al. 2008). Circuitscape models assume that dispersing organisms are analogous to electrical current flowing between discrete nodes over a raster landscape composed of conductors with various amounts of resistance. We used Circuitscape as a modeling framework rather than alternative approaches such as individual-based simulation models (Kanagaraj et al. 2013) or resistant-kernel models (Compton et al. 2007) because our goal was to efficiently evaluate the relative contribution of every location on the landscape to successful dispersal between breeding habitats, for which the modeling framework is well suited (Pelletier et al. 2014).

To parameterize Circuitscape models for each species, we designated the nodes as known areas of breeding habitat (active territory centers for Red-cockaded Woodpeckers, occupied herbaceous wetlands for St. Francis satyr, and temporary ponds for Carolina gopher frog). Because these areas are small relative to the size of the landscape, we represented these locations as point features in the models. We used the empirically derived resistance maps (30-m resolution) to represent the relative resistance of habitat types on the landscape. For each model, each node was sequentially attached to a 1A current source; all other nodes within a species-specific maximum geographic distance were connected to the ground. We summed the resulting current maps across source nodes to create a single map representing the relative density of successfully dispersing organisms (McRae et al. 2008). We considered areas with the highest summed current density the most important for overall population connectivity and used summed current density values as our metric of dispersal habitat quality. To examine the effect on our results of differing assumptions about maximum dispersal distances and habitat occupancy, we also ran the models with no restrictions on maximum dispersal distance and with all potential habitat connected to current sources and grounds, not just occupied habitat (Supporting Information).

Determining Umbrella Effectiveness

We assessed umbrella effectiveness by measuring the amount of spatial overlap in predicted dispersal habitats of differing quality (Fig. 3). To generate a quantitative measure of spatial overlap, we first ranked all cells on the landscape from highest quality to lowest quality according to their modeled relative dispersal frequency. Next, we compared the spatial distribution of dispersal habitats for combinations of our focal species at a large number of equal-area quality thresholds. For example, we compared cells in the top 5% of the landscape for dispersal of species 1 with the top 5% of the landscape for dispersal of species 2 (Fig. 3b). Expressing this quality threshold as a proportion of the landscape, p, instead of a percentage, we computed a spatial overlap coefficient for each combination of species:

$$C(p) = A_{\mathrm{i}}(p)/A_{\mathrm{u}}(p), \tag{1}$$

where $A_{\mathrm{i}}(p)$ is the area of overlap in dispersal habitat between species at the threshold p and $A_{\mathrm{u}}(p)$ is the total area of dispersal habitat above that quality threshold for all species. The resulting measure ranges from 0 (no overlap) to 1 (maximum possible overlap at a given threshold, Fig. 3c). Between these 2 extremes lies an expectation $C^*(p)$, which is the value of $C(p)$ that one would expect if the distributions of dispersal habitat were independent among species:

$$C^*(p) = pS/[1 - (1p)s], \tag{2}$$

where s is the number of species being compared. For a raster landscape with a finite but large number of cells, the numerator of Eq. (2) is equivalent to the proportion of raster cells with habitat in common for all s species if a proportion of cells (p) were drawn at random s times from the set of all raster cells on the landscape. Likewise, the denominator represents the proportion of cells which are selected at least once in s random samples of a proportion, p, of all raster cells. The overlap coefficient must approach 1 because the proportion of the landscape included approaches 1. At lower thresholds, higher values of $C(p)$ relative to the null expectation represent more similar dispersal habitat use among taxa; thus, the more one taxon can serve as a dispersal umbrella for other species. Values of $C(p)$ lower than the null expectation indicate potential conflicts in managing connectivity for multiple taxa and the absence of a good dispersal umbrella species.

Because high-dispersal habitat for any given species is clumped around breeding sites, and thus is spatially autocorrelated, the observed spatial overlap of dispersal habitat between species will differ somewhat from $C^*(p)$ purely by chance, potentially confounding our ability to assess whether spatial distributions of dispersal habitat are truly congruent between taxa. To deal with this issue and create confidence bounds for our expectation of independence, $C^*(p)$, we first created a large number of random raster surfaces with the same extent, resolution, and pattern of spatial autocorrelation as were observed in our models of dispersal density. We then computed 2-species and 3-species overlap coefficients for 300 unique combinations of these random surfaces and measured the frequency of the resulting values of $C(p)$ across all combinations of surfaces. We considered an observed value of $C(p)$ biologically meaningful if it fell outside the 97.5% and 2.5% quantiles computed from overlapping random surfaces. Further details about the null modeling approach are in Supporting Information.

Results

Despite the study species having widely divergent breeding habitats, they shared some overlap in their dispersal habitats, such that all 3 species could serve as connectivity umbrella species for the others. One type of habitat (upland forest) was the most likely to be used for dispersal between breeding habitat patches for all 3 target species, and it constituted 60%–80% of the most important dispersal habitat (i.e., the 5% of the landscape with the highest dispersal density). In contrast, open and developed environments contributed relatively little (15%–30%) to the highest value dispersal habitats. Some areas were important for the dispersal of all 3 species (Fig. 2b) and represented portions of the landscape where breeding habitats and predicted dispersal paths existed in close proximity.

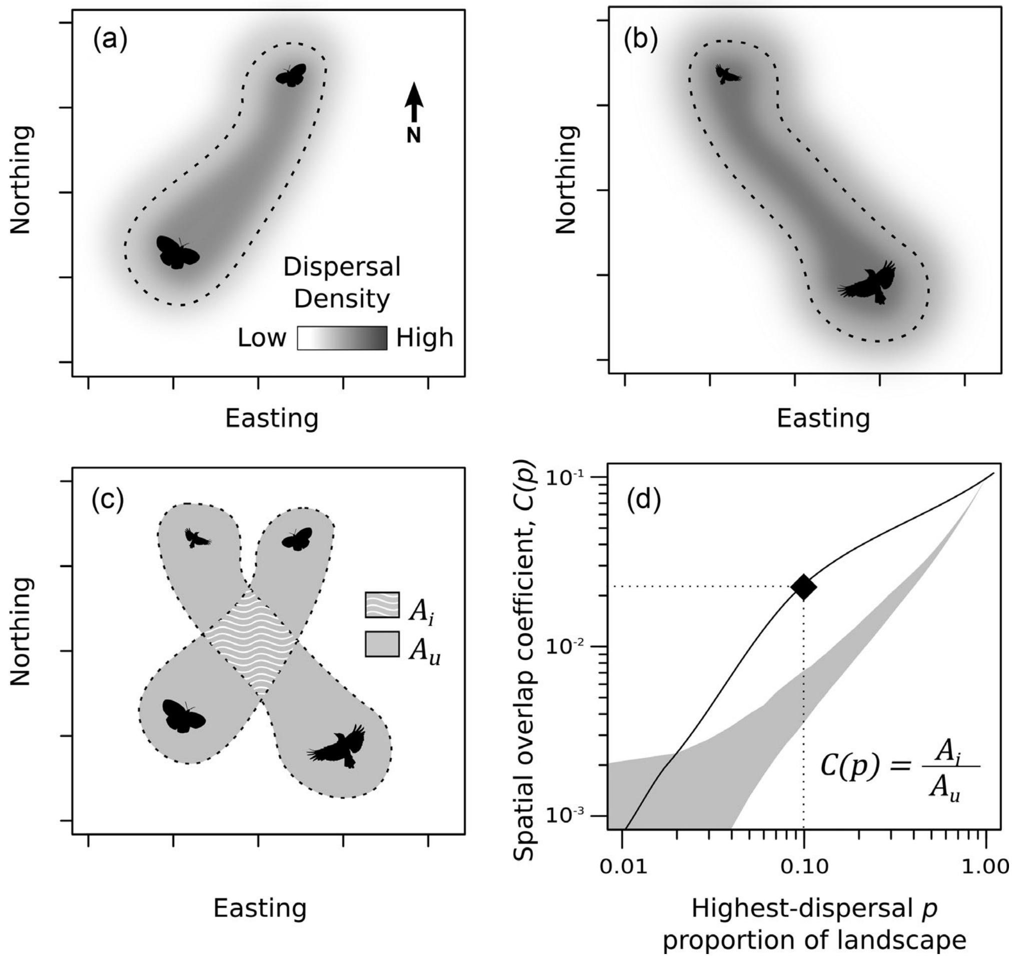

Figure 3. Methods used in this analysis to quantify spatial overlap of dispersal habitat for hypothetical species 1 and 2. (a) and (b) Maps of the relative density of dispersal for the 2 species (darker colors, more frequent dispersal; dotted black lines, enclose areas above a relative dispersal frequency threshold, p, for each species). These maps are overlayed in (c) to show areas above the density threshold for both species simultaneously (areas of intersection, A_i) and areas above the threshold for either species (areas of union, A_u). (d) Spatial overlap coefficient C(p) for each threshold based on the values of A_i and A_u in (c). If the observed value of C(p) at a given threshold is above the gray shaded region, then dispersal areas for the 2 species overlap more than would be expected by chance at that threshold, providing opportunities for management synergy. In this example, $p = 0.1$, indicating that the overlap analysis compares the 10% of the landscape with the highest relative dispersal density for each species.

Umbrella Effectiveness

Dispersal habitat overlapped significantly more than would be expected by chance alone for all pairs of species, regardless of what proportion of the landscape was considered (Figs. 4a and 4b). Overall, the butterfly and the frog had the most congruent patterns of dispersal habitat use. Spearman's rank correlation coefficients between Circuitscape current density values (our proxy for dispersal frequency) at points on the landscape were positive across all pairs of species (0.52, 0.50, and 0.67 for bird and butterfly, bird and frog, and butterfly and frog, respectively). The frog had the highest average correlation with the other species when correlation coefficients were averaged across the model scenarios we considered (Supporting Information). In contrast, dispersal habitat use for the Red-cockaded Woodpecker, currently used as an umbrella species for conservation in this landscape, was the most weakly correlated with that of the other species, a result that was not sensitive to our selection of analysis area or dispersal model parameterization (Supporting Information).

Synergy or Conflict

Dispersal habitat overlapped significantly more than would be expected by chance when all 3 species were considered together (Fig. 4b), indicating that synergy among the 3 species was more common than conflict. For example, if the distributions of dispersal habitat for

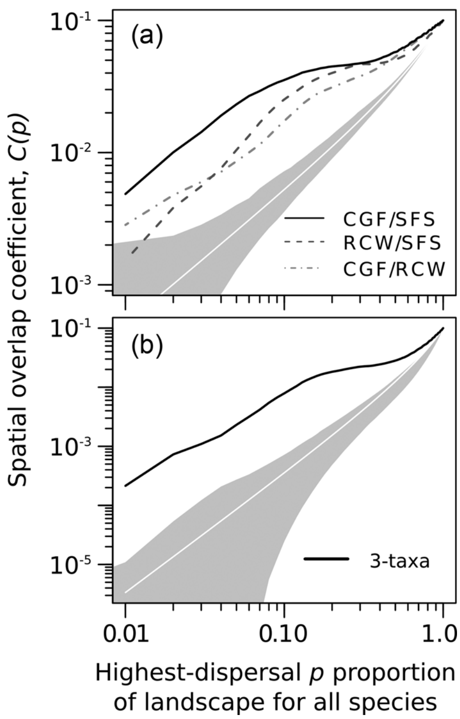

Figure 4. Spatial overlap of important dispersal areas as a function of the relative dispersal density threshold, p: *(a) overlap between each pair of species (RCW, Red-cockaded Woodpecker; CGF, Carolina gopher frog; SFS, St. Francis saytr) and (b) overlap of all 3 species simultaneously . Gray shading represents 2.5% and 97.5% quantiles from the spatial null model, indicating overlap at that threshold might be expected by chance with no association in dispersal habitats among species; white line represents the analytical expectation from Eq.* 2.

the species were completely independent of each other, we would expect that just 0.1% of the landscape would be in the top 10% of dispersal habitat for all 3 species. The actual overlap of dispersal habitat was an order of magnitude larger (2.4% of the landscape) than would be expected by chance alone. Our analysis of alternative scenarios (Supporting Information) indicated that our overall conclusion is robust to our assumptions about the locations of breeding habitats and the maximum dispersal distance.

Important dispersal areas for the 3 species existed almost entirely on lands currently managed for wildlife (Fig. 2b). Because unprotected private lands do not contribute significantly to multispecies connectivity, we repeated the analysis of overlap considering only areas that were managed for wildlife (Supporting Information). The results were qualitatively similar to the results when we considered the entire landscape; however, the overall degree of spatial overlap was closer to the null expectation. For example, when we examined spatial overlap of the top 10% dispersal habitat on managed lands, 0.3% of those managed lands were important for all 3 species, compared with a null expectation of 0.1% if the distributions were independent.

Discussion

Dispersal habitat for the 3 target species typically overlapped more than, and never overlapped less than, the proportion predicted by a null model. Our results suggest that areas of connectivity management synergy do exist and can contribute to connectivity conservation for diverse taxa. More generally, we contend that the umbrella species concept is likely to be useful in connectivity conservation and that even suites of species with very different spatial patterns of breeding and foraging habitat may nonetheless use similar portions of the landscape for dispersal. If we had chosen a group of focal species that, like Red-cockaded Woodpeckers, all breed in and disperse through the same types of environments, spatial overlap in dispersal habitat would almost certainly have been higher. Although dispersal habitats of the 3 species were more similar than are their breeding habitats, we found important dispersal differences. Most importantly, dispersing Red-cockaded Woodpeckers avoided forested wetland, where the butterfly preferentially disperses (and breeds), whereas dispersal areas for the frog bridge both riparian and upland environments. For the 3 species we considered, we also did not find evidence of major conflicts in conserving dispersal habitat (Fig. 1d). One might naively expect that such trade-offs or conflicts would not arise among species on their native landscape, where extensive disturbance and spatially varied habitats across the landscape may have enhanced the dispersal capacities of a variety of species. However, especially because humans have modified landscape configuration and dynamics, current habitat configurations may create trade-offs that have not always existed.

Typically, conservation biologists assume that species with large body size (e.g., carnivores) will require large home ranges, which therefore will encompass the habitat needs of smaller bodied species. However, we found that the largest bodied species (the woodpecker) did not serve as the best connectivity umbrella, mirroring other studies (Beier et al. 2009; Cushman & Landguth 2012). Even simple information about which species use which habitats during dispersal could help identify the species (e.g., the frog in our study) whose dispersal needs resemble those of the greatest number of other threatened species on the landscape. A still more powerful approach would be to simulate species with a range of dispersal behaviors and geographic distributions to identify key characteristics that might make a given species a good umbrella for connectivity. Cushman and Landguth (2012) used this approach to identify traits of good connectivity umbrella species on a landscape in western North America. They found that both far-dispersing species and habitat generalists performed relatively well as connectivity umbrellas compared with other taxa.

Although studies with a large number of simulated species are useful in identifying traits that might make species suitable connectivity umbrellas, our approach for evaluating connectivity umbrellas is likely to be generally useful when dispersal data for multiple focal species are available. Our approach is flexible in terms of how dispersal and resistance to dispersal are measured. We obtained values for resistance in different ways: for frogs and butterflies by tracking detailed movement paths and for woodpeckers by following radio-tagged birds and measuring dispersal of banded individuals. Expanding our analysis to a wider array of species in this landscape could serve to identify traits of a species that influence its relative performance as a connectivity umbrella.

We identified areas supporting the highest expected frequency of dispersal between breeding habitats. These predicted high-traffic areas are likely to be used by many animals, but we do not identify dispersal paths that are used by rare long-distance dispersers that may be disproportionately responsible for determining patch occupancy and persistence in fragmented landscapes (Johst et al. 2002). Although conditions that facilitate routine and rare long-distance dispersal are often thought to be similar, this assumption is difficult to test. Further, we identified areas that are currently important for dispersal of multiple taxa, but we did not explicitly identify areas where habitat restoration could provide the greatest increase in multispecies connectivity. To our knowledge, this is an unexplored area of research. However, McRae et al. (2012) developed promising tools for detecting movement barriers and connectivity restoration opportunities, and this approach could be applied in a variety of landscapes to assess whether management synergies are common for connectivity restoration, as well as conservation across taxa.

Our approach to assessing multispecies connectivity shows both the promise and limitations of extending the umbrella species concept to landscape connectivity. We found that the concept can be used to identify species that, if used to guide habitat management, would lead to protection of areas important for the dispersal of a suite of rare and taxonomically diverse species threatened by habitat fragmentation. Nonetheless, our results also make clear that no one species is a perfect surrogate for the others. Furthermore, our findings cast doubt on the implicit assumption that the largest bodied species with the largest home range and dispersal capacity in a landscape is the best umbrella. At least some basic knowledge of the dispersal habitats used by the species of concern may be necessary to decide which species are likely to fall safely under the umbrella of another. In sum, the umbrella species concept can be effectively applied to connectivity if done carefully, with an understanding of how a variety of species disperse across the landscape.

Acknowledgments

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Supporting Information

Details regarding the processing of spatial habitat data (Appendix S1), estimation of landscape resistance values for each species (Appendix S2), the spatial null modeling approach (Appendix S3), and sensitivity analysis (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

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