

RESERVE NETWORKS BASED ON RICHNESS HOTSPOTS AND REPRESENTATION VARY WITH SCALE

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Abstract. While the importance of spatial scale in ecology is well established, few studies have investigated the impact of data grain on conservation planning outcomes. In this study, we compared species richness hotspot and representation networks developed at five grain sizes. We used species distribution maps for mammals and birds developed by the Arizona and New Mexico Gap Analysis Programs (GAP) to produce 1-km², 100-km², 625-km², 2500-km², and 10 000-km² grid cell resolution distribution maps. We used these distribution maps to generate species richness and hotspot (95th quantile) maps for each taxon in each state. Species composition information at each grain size was used to develop two types of representation networks using the reserve selection software MARXAN. Reserve selection analyses were restricted to Arizona birds due to considerable computation requirements. We used MARXAN to create best reserve networks based on the minimum area required to represent each species at least once and equal area networks based on irreplaceability values. We also measured the median area of each species' distribution included in hotspot (mammals and birds of Arizona and New Mexico) and irreplaceability (Arizona birds) networks across all species.

Mean area overlap between richness hotspot reserves identified at the five grain sizes was 29% (grand mean for four within-taxon/state comparisons), mean overlap for irreplaceability reserve networks was 32%, and mean overlap for best reserve networks was 53%. Hotspots for mammals and birds showed low overlap with a mean of 30%. Comparison of hotspots and irreplaceability networks showed very low overlap with a mean of 13%. For hotspots, median species distribution area protected within reserves declined monotonically from a high of 11% for 1-km² networks down to 6% for 10 000-km² networks. Irreplaceability networks showed a similar, but more variable, pattern of decline.

This work clearly shows that map resolution has a profound effect on conservation planning outcomes and that hotspot and representation outcomes may be strikingly dissimilar. Thus, conservation planning is scale dependent, such that reserves developed using coarse-grained data do not subsume fine-grained reserves. Moreover, preserving both full species representation and species rich areas may require combined reserve design strategies.

Key words: biodiversity; conservation planning; grain; hotspots; map resolution; MARXAN; representation; reserve selection; selection algorithms; spatial scale, species richness.

INTRODUCTION

Identifying and understanding biodiversity pattern in nature is a central theme in ecology and is becoming increasingly important in conservation science (Crawley and Harral 2001). Rapid human population growth and its concomitant threats to biodiversity—land conversion (Flather et al. 1997), fragmentation (Saunders et al. 1991), invasive species (Pimentel et al. 2000), and climate change (Hansen et al. 2001)—combined with scarce conservation dollars, underscore the need to protect the earth's biota quickly and efficiently. Accelerating threats

to biodiversity require rapid development of conservation plans to avert species extinctions and prevent lost opportunities due to land alteration. Further, diverse land use pressures necessitate the establishment of efficient reserve networks that minimize area requirements for protecting biodiversity.

Two of the most common strategies used to establish priority areas for targeting conservation efforts are delineation of species richness hotspots and the development of complementary reserve sets based on the notion of species representation. Both approaches rely on the creation of species richness maps developed by overlaying species distribution maps. Due to the lack of detailed data on species distributions over broad areas, species richness maps are often relatively coarse grained with the size of the minimum planning unit frequently 10 000 km² or greater (e.g., Andelman and Willig 2002, Larsen and Rahbek 2003, Moore et al. 2003). Con-

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servation planning based on these data, and therefore the grain size of conservation planning outcomes, is often far more coarse than can be practically implemented (Pressey and Logan 1998, Hopkinson et al. 2000, Ferrier 2004); i.e., reserve sizes greater than 10 000 km² are relatively rare. While large reserves may be desirable for many reasons, land availability and increasing parcelization limit the potential size of new reserves (Hopkinson et al. 2000, Walsh et al. 2004). Andelman and Willig (2003) analyzed the size distribution of protected areas in the Western Hemisphere and found that median reserve size was 4.86 km² and fewer than 3% of reserves were larger than 5000 km². A mismatch between the grain size underlying conservation planning analyses and the grain size of conservation implementation is problematic if conservation planning results are scale dependent such that reserve networks identified with fine-grained analysis overlap little with those identified at coarser grains.

Unfortunately, detailed species range data are not generally available over broad regions (Rahbek and Graves 2001, Andelman and Willig 2002). Therefore, ecologists have little choice but to use coarse-grained data. Rahbek and Graves (2000) report that more than 50 papers addressing biodiversity pattern have been based on distribution data at grain sizes exceeding 500 000 km². Many authors that use coarse-grained data either implicitly assume patterns detected using coarse-grained data reflect those at other grains (Rahbek and Graves 2000, Larsen and Rahbek 2003) or fail to discuss potential consequences of extrapolating results to other scales. Nonetheless, ecologists long ago recognized scale dependencies in diversity patterns (see Rahbek and Graves 2000, He et al. 2002, and Rahbek 2005 for historical citations). Unfortunately, this scale dependence is often ignored in macro-ecological and conservation planning studies (Rahbek and Graves 2000). Despite a growing body of empirical evidence highlighting the fact that map grain affects species richness patterns (e.g., Palmer and White 1994, Stoms 1994, Stohlgren et al. 1997, Lennon et al. 2001, He et al. 2002) and the reliance of many conservation planning approaches on species richness information, discussion and analysis of the impact of map grain on conservation planning outcomes are relatively uncommon.

Many researchers and practitioners have acknowledged the need for multi-scaled approaches to conservation planning, but most conservation planning analyses are performed at a single scale. Further, the call for multi-scaled approaches is not generally coupled with a call to explicitly address the impact of data resolution on conservation planning outcomes (e.g., Donovan et al. 2000, Poiani et al. 2000, Lambeck and Hobbs 2002, Bestelmeyer et al. 2003, Groves 2003, Noss 2004). Although data availability is certainly a constraint that limits multi-scale planning applications, conservation plans cannot be appropriately implemented without an understanding of how biodiversity

attributes change across scales. Stoms (1994) showed that, while species richness maps generally maintain identifiable patterns across spatial scales, species richness is not nested across grain sizes and does not necessarily vary in predictable ways. This result is a function of the fact that species richness is nonadditive when small units are aggregated into larger units (He and Legendre 1996, Legendre and Legendre 1998, He et al. 2002) because the degree of compositional similarity between units varies when the focus is on species counts. Nesting is not expected because, as Stoms (1994) explains, the aggregation of species richness areas is the logical union of combined sets rather than the mean of combined sets. The fact that species richness cannot be expected to nest across data grains clearly limits our ability to generalize results across spatial scales and has important implications for conservation planning.

In this study, we investigated the spatial overlap of reserve networks developed at five grain sizes. We assessed the impact of data grain on reserve networks based on species richness hotspots and species representation by systematically developing reserve networks at each grain and then comparing the spatial overlap of those reserves. If reserve networks developed at different grain sizes show high spatial overlap, implementing conservation planning outcomes at a grain other than the analysis is tenable. However, if reserve networks do not overlap, caution must be applied when reserve networks are designed at grain sizes different from the grain of implementation. We also compared the congruence of hotspot networks developed for different taxa as well as the congruence of networks based on species richness hotspots and species representation. Coincidence of networks developed for different taxa supports the use of surrogate taxa in conservation planning whereas a lack of coincidence implies networks developed for a single taxon are unlikely to adequately protect other taxa. High spatial overlap between networks based on species richness hotspots and species representation suggests that a single conservation planning approach may meet multiple conservation goals when both species representation and protection of species-rich areas are desired. However, low spatial overlap between these two types of networks indicates conservation planners must carefully prioritize conservation goals or develop methodologies that simultaneously achieve multiple goals.

We also compared the median area protected for individual species in reserve networks developed at different map grains. The area protected for a given species is an important characteristic of reserve networks because as the amount of area protected increases, long-term persistence is likely to increase. We hypothesized that, because fine-grained maps can better match species distribution boundaries, on average, conservation planning outcomes based on fine-grained maps would result in increased area of

protection for individual species compared with outcomes based on coarse-grained maps.

METHODS

Richness hotspot reserves

We used species range maps for mammals and birds developed by the Arizona and New Mexico Gap Analysis Program (GAP) projects completed in 1999 and 1996, respectively (Thompson et al. 1996, Halvorson et al. 2001). While these maps undoubtedly contain errors (Dean et al. 1997), we used them as simulations of “true” communities of co-occurring species that represent a range of distribution characteristics. Our analyses required known distributions so that we can appropriately isolate the effects of grain size without confounding differences in spatial overlap due to map error.

The Arizona GAP distribution maps were available as shape files based on 90×90 m grids and New Mexico maps are available as 100×100 m rasters (the study area location is shown in the inset map for Fig. 3). We used ESRI ArcGIS 8.2 (ESRI, Redlands, California, USA) to convert each species range map for mammals and birds in each state to raster format at five different map grains: 1×1 km (1 km^2), 10×10 km (100 km^2), 25×25 km (625 km^2), 50×50 km (2500 km^2), and 100×100 km (10000 km^2). Grid placement was held constant across grains (i.e., each map was developed based on the same lower-left coordinates) in this and all subsequent analyses. We created distribution grids at each of the five grain sizes based on binary, i.e., presence-absence, information such that any species range overlap with a grid cell counted as distribution area. We did not use a resampling (interpolation) approach because resampling assumes information is known at finer grains and is not typical of the application of occurrence data in the generation of distribution maps.

We generated species richness maps for birds and mammals in each state at each grid cell resolution by overlaying the relevant species distribution maps. To discern potential effects of taxa-specific range characteristics on our analyses, we did not combine data across taxa. We used these species richness maps to develop hotspot maps. In general, we defined hotspots as grid cells exceeding the 95th quantile for number of species represented within a grid cell as in Prendergast et al. (1993). This criterion results in the identification of reserve networks that represent 5% of the area of the extent under investigation. However, when multiple grid cells can have the same value, quantiles occur at discrete breakpoints and do not necessarily occur precisely at the 95th quantile. In an effort to create hotspot reserve networks that were as similarly sized as possible at the different grain sizes, we chose the quantile break closest to the 95th quantile that minimized area differences between maps developed at different grain sizes. For Arizona hotspots maps, hotspots centered on the 95th quantile (range, 94.24–95.39) and for New Mexico

hotspot maps, hotspots centered on the 94th quantile (range, 93.46–94.12).

In total, we created hotspot maps for four groups: Arizona birds (279 species), New Mexico birds (324 species), Arizona mammals (129 species), and New Mexico mammals (138 species). For each group we created 20 maps representing five different grain sizes. The number of potential planning units (grid cells) varied greatly with grain size. For example, the Arizona maps ranged from 41 potential planning units for the 10000-km^2 maps to 296 327 potential planning units for the 1-km^2 maps. For comparative purposes, it should be noted that the 100-km^2 map grid cells are not nested within the 625-km^2 map grid cells; however, all other grain size comparisons represent a nested pair.

Representation reserves

We created reserve networks for Arizona birds at five grains using the species composition maps developed in the previous section as input data for the reserve selection software MARXAN 1.8.2 (Ball and Possingham 2000). We focused on Arizona birds because the numerical intensity of the MARXAN reserve selection algorithms did not permit a comprehensive analysis across both taxa and states. Representation has become a relatively common approach to reserve selection for both terrestrial and marine systems (e.g., Leslie et al. 2003, Warman et al. 2004, Cook and Auster 2005). The basic objective of reserve selection based on representation is to attain a set representation goal for conservation features (e.g., species, populations, or vegetation types) at minimum cost, which is generally minimum area (Pressey et al. 1993, Possingham et al. 2000, Leslie et al. 2003). When reserve selection occurs over a broad area encompassing a large number of potential sites, identifying reserve configurations that efficiently meet representation goals requires computer-based methods (Possingham et al. 2000, Leslie et al. 2003).

MARXAN offers several spatially explicit algorithms for solving minimum representation problems (Ball and Possingham 2000). Among them, simulated annealing has been shown to perform well (Possingham et al. 2000) and to provide multiple solutions which offer flexibility for conservation planning. Simulated annealing minimizes an objective function by simulating the process of annealing metals or glass (Kirkpatrick et al. 1983, Possingham et al. 2000). The algorithm proceeds by forming an initial reserve by randomly selecting a suite of sites. Sites selected randomly (with replacement) are then added or removed from the group of sites. The value of the objective function for each new group is compared with the previous solution and is either accepted or rejected. The criterion for acceptance becomes increasingly stringent as the algorithm progresses such that initially suboptimal changes may be selected, but toward the end of the process only advantageous changes are accepted. The progressively stricter acceptance criterion allows the algorithm to

avoid local minima, increasing the likelihood that the global optimum is identified.

MARXAN uses simulated annealing to identify a near optimal set of reserves by minimizing an objective function (total cost) based on full representation of conservation features and other conservation criteria (species weights, economic cost of planning units, boundary length, etc.). The MARXAN objective function is

$$\text{total cost} = \sum_{\text{PUs}} \text{PU costs} + \text{BLM} \sum_{\text{PUs}} \text{boundary lengths} \\ + \sum_{\text{species}} \text{CFPF} \times \text{penalty} \times \text{threshold penalty}$$

where PU is planning units (grid cells), BLM is the boundary length modifier, and CFPF is the conservation features penalty factor. The boundary length modifier is a weighting factor that can be used to spatially aggregate planning units, the conservation feature penalty factor is the penalty associated with failing to represent a conservation feature, and the threshold penalty is a cost associated with exceeding a set maximum number of planning units or cost.

Because our goal was to compare reserve networks developed at different map grains rather than to develop actual conservation networks, we used a relatively simple set of conservation priorities. We set all conservation features (species) and planning units (grid cells) to equal weight (cost) to reflect uniform species priority and land acquisition costs. We set the representation target to a minimum of one representation of each species and we did not use a boundary length modifier to reduce fragmentation because the desired level of spatial aggregation of reserve sites would vary with spatial grain. We processed 1000 runs for each of the five grain-size data sets using simulated annealing followed by iterative improvement as the solution method. Iterative improvement removes duplicated or inessential planning units, thus improving the likelihood of identifying an optimal solution (Ball and Possingham 2000).

We created two types of reserve networks based on the MARXAN output. First, we identified the best reserve system for each grain size. The best reserve network for a given grain size is the best solution found across the 1000 runs and corresponds to the minimum cost (in this case, minimum area) reserve identified that includes at least a single representation of each species. Best reserve networks prescribed at each grain size vary greatly in size with large-grained data leading to larger total reserve network area. These size differences confound interpretation of scale effects because reserves are more likely to overlap as reserve size increases. Therefore, we created a second type of representation reserve network based on irreplaceability values in order to delineate approximately equal-area reserves. In general, we defined irreplaceability networks as all grid cells exceeding the 95th quantile for irreplaceability

values. The irreplaceability score for a given planning unit is the number of times the grid cell is selected as a member of the best reserve in each of the individual 1000 runs and therefore varies from 0 to 1000. As with species richness hotspots, multiple grid cells can have the same irreplaceability value so we chose quantile breaks that minimized differences (range, 94.91–95.17).

The primary goal of representation-based reserve selection is to attain a specified number of representations of each conservation feature (species) at minimum cost (area). Therefore, in developing irreplaceability reserves we maximized species representation in the reserves even if this criterion meant choosing a grid cell with an irreplaceability score below the 95th quantile. Given area constraints, the 10 000-km² and 2500-km² irreplaceability reserves were smaller than the best reserves, so we could not achieve full species representation. The 625-km² and 100-km² irreplaceability reserves were larger than the best reserves so we first insured full species representation for these networks by selecting the best set and then adding additional grid cells to reach the 5% reserve area criterion based on irreplaceability scores. This scheme resulted in the inclusion of four grid cells with irreplaceability scores below the 95th quantile for the 625-km² reserve and a single grid cell below the 95th quantile for the 100-km² reserve. We did not develop an irreplaceability reserve network for the 1-km² grid because too few cells were selected across the 1000 runs to meet the 5% area goal.

Scale comparisons

We examined the effects of grain size by comparing five groups of reserve networks. (1) We compared spatial overlap between species richness hotspot reserve networks developed for each grain size (four groups: Arizona birds, New Mexico birds, Arizona mammals, and New Mexico mammals). (2) We compared spatial overlap between species richness hotspot reserve networks generated for different taxa (birds vs. mammals) at each grain in each of the two states. For representation reserve networks, we compared (3) best networks developed at each grain size and (4) irreplaceability networks developed at each grain size. (5) Finally, we compared spatial overlap between species richness hotspot reserve networks and irreplaceability reserve networks.

We compared richness hotspot reserves, best reserves, and irreplaceability reserves by calculating the spatial overlap between each pair of reserve networks generated at the five scales. Hotspot and irreplaceability reserve networks represent approximately 5% of the area of the states. Because the final area of these reserve networks was not exactly 5% and because best networks produced at different grains have unequal areas, we used the area of the smaller reserve network as the denominator in overlap calculations; i.e., percentage overlap = (area of spatial overlap/area of the smaller of the two reserves) × 100. We chose the smaller area to insure that percen-

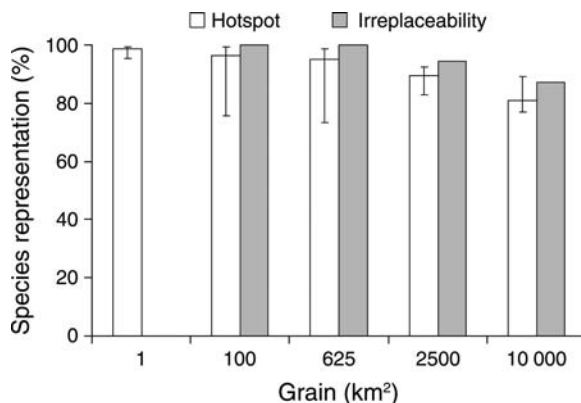


FIG. 1. Species representation in species richness hotspot reserve networks and irreplaceability reserve networks. For the species richness hotspot reserves, each bar is a mean based on representation in hotspots for Arizona birds, New Mexico birds, Arizona mammals, and New Mexico mammals. Error bars represent the minimum and maximum representation across the four groups. We did not create a 1-km² irreplaceability reserve network because too few planning units received irreplaceability scores to develop an equal area network at this grain size.

tages varied from 0 to 100. The area of best reserve networks increases with increasing grain size. Therefore, computation of percentage overlap between grain sizes for these networks represents the degree to which a smaller reserve network is nested within the larger reserve network.

For comparative purposes, we also report an adaptation of Jaccard's similarity coefficient for measuring spatial overlap (van Jaarsveld et al. 1998, Warman et al. 2004), which has been applied in previous studies. In this version of the index, Jaccard's similarity coefficient = area of spatial overlap / (area of spatial overlap + non-overlapping area of reserve one + non-overlapping area of reserve two). While this coefficient may be construed as percentage overlap, it is different from our simple percentage because this definition of overlap uses the union area of two reserve networks in the denominator rather than the area of a single reserve network. This index can be somewhat misleading as an indicator of spatial overlap when the reserve networks being compared have unequal areas. For example, in a comparison between a species richness hotspot network and a representation reserve network, Dimitrakopoulos et al. (2004) report 8.42% spatial overlap between the two networks based on Jaccard's Index. This low overlap is due to the large size differential between the two networks and obscures the fact that the richness hotspot network is completely nested within the representation network.

Area protection for individual species

We calculated the median area of a species' distribution that is protected within equal area reserve networks across all individual species. We used this metric as a surrogate measure of the relative likelihood of persis-

tence for individual species within a reserve network based on the assumption that the likelihood of persistence increases as species' range area (and presumably abundance) increases within a reserve network. For each richness hotspot and irreplaceability reserve network described above, we determined the area of each individual species' distribution contained within a reserve network. We converted areas to the percentage of each species' distribution area that occurred in a reserve network based on the total distribution area for a species in the state of the reserve network.

Global reserve size

We evaluated the size distribution of protected areas across the globe to gain an understanding of the likelihood of implementing reserve networks developed at different grain sizes. We used the 2004 World Database on Protected Areas (World Database on Protected Areas Consortium 2004) to determine the median size of reserves across the globe. The database is not a complete census of protected areas due to lack of appropriate geographic information for some areas and limitations on distributing data (World Database on Protected Areas Consortium 2004). Nonetheless, the database is the best available information on protected areas of the world. Following the lead of Andelman and Willig (2003), we limited our analyses to reserves classified by the World Conservation Union (IUCN) as category I or II because the chief purpose of these categories of protected areas is conservation. This approach excludes reserves that undoubtedly provide conservation value, such as protected areas that allow resource extraction (e.g., National Forests) while retaining some areas that provide little biodiversity value (e.g., National Monuments). However, the vast array of reserve classification systems used in different nations and variation in enforcement of particular reserves precludes easy categorization. We limited our analyses to wholly terrestrial reserves and eliminated reserves with areas ≤ 1 ha because a large proportion of these very small reserves protect historic monuments and/or isolated geologic formations. We also deleted all duplicate records that occurred within a single country.

RESULTS

In general, species richness hotspots contained a high proportion of the total species pool for a given group and the number of species represented in richness hotspot reserves increased as grid cell size decreased (Fig. 1). Mean species representation in richness hotspot reserve networks was 81.1% (range, 76.8–89.2) for 10000-km² grid maps and 97.95% (range, 95.7–99.4) for 1-km² grid networks. Within state-taxon groups, pairwise comparisons of richness hotspot reserve networks generated from species richness maps of different grain sizes showed relatively low spatial overlap (Table 1, Appendix). Percentage overlap over all comparisons and groups ranged from 0.0% to 63.1% with a grand

TABLE 1. Pairwise comparisons of overlap for richness hotspot reserves developed at five grain sizes: 1 km², 100 km², 625 km², 2500 km², and 10 000 km².

Map comparison (km ²)	Arizona		New Mexico	
	Percentage overlap†	Jaccard's coefficient	Percentage overlap†	Jaccard's coefficient
Birds				
10 000, 2500	16.7	8.5	37.5	23.1
10 000, 625	21.9	11.1	18.8	10.3
10 000, 100	26.5	13.8	11.2	6.0
10 000, 1	33.4	18.5	13.0	7.1
2500, 625	17.6	9.4	34.1	20.7
2500, 100	27.8	15.8	21.4	12.2
2500, 1	14.6	7.8	19.6	11.1
625, 100	47.1	30.6	42.7	27.5
625, 1	25.1	14.0	18.4	10.3
100, 1	32.7	19.2	29.4	17.3
Mean	26.3	14.8	24.6	14.5
Mammals				
10 000, 2500	17.8	8.7	50.0	33.3
10 000, 625	0.0	0.0	25.3	14.4
10 000, 100	0.0	0.0	12.4	6.3
10 000, 1	5.1	2.4	8.7	4.3
2500, 625	54.5	34.1	56.9	39.4
2500, 100	43.4	26.5	36.1	21.0
2500, 1	27.7	15.9	21.8	11.7
625, 100	63.1	44.0	50.2	32.1
625, 1	40.5	23.6	23.9	13.1
100, 1	57.8	39.2	36.2	22.1
Mean	31.0	19.4	32.1	19.8

Note: See Appendix for associated figures.

† Percentage overlap is calculated by dividing the area of overlap by the area of the smaller reserve.

mean of 28.6%. Mean percentage overlap at different grain sizes was lower for birds (grand mean across both states = 25.6%) than for mammals (grand mean across both states = 31.6%), but was very similar across the two taxa within the two states (28.7% for Arizona and 28.6% for New Mexico).

Comparisons of spatial overlap of richness hotspot reserve networks developed for birds and mammals were based on networks developed at the same grain sizes and in the same state; e.g., the 1-km² bird richness hotspot map for Arizona was compared to the 1-km² mammal hotspot map for Arizona (Table 2, Appendix). Mean percentage overlap between mammal and bird richness hotspots across the five grains was 39.6% (range, 33.8–51.7%) in Arizona and just over half that at 20.4% (range, 0.0–35.1%) in New Mexico. Percentage overlap between the Arizona taxa showed no discernable pattern as a function of grid cell size, whereas overlap in New Mexico decreased monotonically with increasing grid cell size.

Representation reserves

Reserve size increased dramatically with increasing grain size for best reserve networks generated for Arizona birds (Fig. 2). Best reserve networks represent minimum area networks identified in MARXAN that contain at least a single representation of each species. The best reserve network developed from the 1-km²

TABLE 2. Spatial overlap between richness hotspot reserves developed for mammals and birds.

Grid cell size (km ²)	Arizona		New Mexico	
	Percentage overlap†	Jaccard's coefficient	Percentage overlap†	Jaccard's coefficient
10 000	41.2	26.0	0.0	0.0
2500	35.5	20.8	12.5	6.7
625	51.7	32.0	24.7	13.9
100	35.6	21.0	29.7	16.4
1	33.8	19.9	35.1	19.9
Mean	39.6	23.9	20.4	11.4

Note: See Appendix for associated figures.

† Percentage overlap was calculated by dividing the area of overlap by the area of the smaller reserve.

species composition data represents just under 0.01% (28 km²) of the area of Arizona. On the other hand, the best reserve network created from the 10 000-km² species richness data occupies nearly 20% (58 578 km²) of the state. Spatial overlap of best reserve networks developed for different grains varied from 26.6% to 69.9% with a mean of 54.5% (Fig. 3).

Irreplaceability reserve networks based on the top 5% of irreplaceability values show low spatial overlap for networks developed from species composition data at different grains (Fig. 4). Percentage overlap varied from 15.3% to 44.2% with a mean of 23.9%. Although area overlap was relatively low, reserve sites tended to cluster together in specific areas of the state. In many areas where reserve networks developed at different grain sizes did not overlap, grid cells in one network were adjacent or very near those in another network. Representation within irreplaceability reserve networks was not complete for the 10 000-km² and the 2500-km² reserves due to the area restriction imposed by selecting cells that exceeded the 95th quantile (Fig. 1). The 10 000-km² reserve set contained 243 out of 279 species, or 87.10% of the species pool and the 2500-km² reserve set represented 263 out of 279 species, or 94.27%. Because we prioritized species representation for the irreplace-

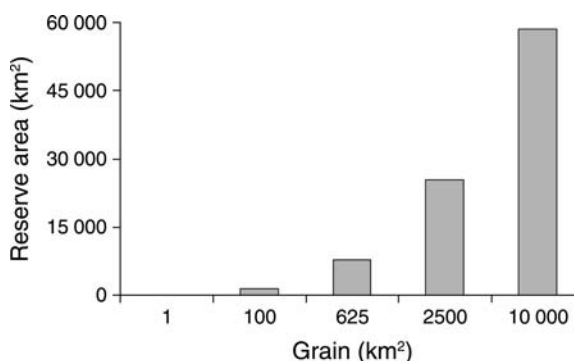


FIG. 2. Reserve area of best reserve networks developed at five grain sizes for Arizona birds. The 1-km² reserve size is 28 km². Each best reserve network contains a minimum of one representation of each species.

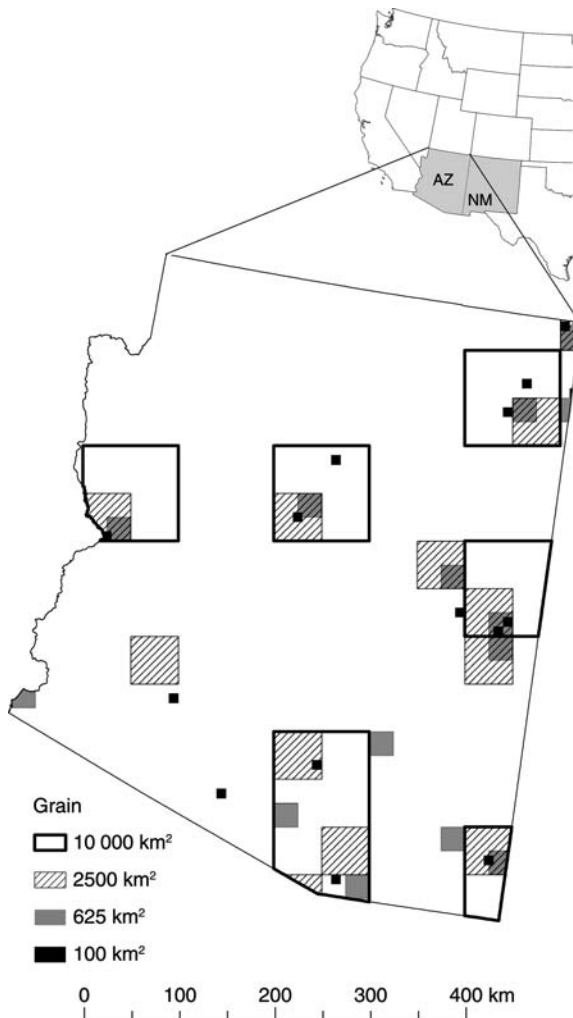


FIG. 3. The small map shows the western United States with Arizona (AZ) and New Mexico (NM) in gray. The magnified map shows the spatial overlap of best reserve networks for AZ birds based on four map grains. The 1-km² network is too small to be seen. Best reserves are the minimum area solution to full species representation found in 1000 MARXAN runs.

ability reserves, the 625-km² and 100-km² reserves had full species representation.

An assessment of irreplaceability scores showed large differences in planning unit irreplaceability as a function of grain size (Fig. 5). The 1-km² analysis showed few reserve sites have high irreplaceability values with very few planning units chosen more than 10% of the time and most chosen in fewer than 2% of the runs. In contrast, the 10 000-km² irreplaceability analysis shows very high irreplaceability scores. All seven planning units selected for the best reserve network were chosen in 100% of the runs, indicating that no other combination of sites would represent all species with minimum area. The irreplaceability analysis also showed that the simulated annealing algorithm produced fairly consis-

tent results. Across the 1000 runs for each grain size, the sites chosen for best reserves represent a relatively small portion of those available. For the 10 000-km² analysis, 75.6% of grid cells were never selected in any of the 1000 runs and for the 100-km² analysis, 99.4% of grid cells were never selected.

Richness hotspot and irreplaceability reserve networks

Reserve networks based on species richness hotspots showed very low spatial overlap with irreplaceability networks (Fig. 6). Mean percentage overlap was 13.1% across the four different grain size comparisons. Spatial overlap for the 100-km² networks was 10.1%, with 24.6% overlap for the 625-km² networks, 17.5% overlap for the 2500-km², and 0.0% overlap for the 10 000-km² reserves. As expected, irreplaceability reserve networks represented more species than richness hotspot reserve networks. However, richness hotspot networks included a relatively high proportion of species, with all but five species represented in the finest grained 1-km² reserve (Fig. 1).

Area protection for individual species

In general, the area percentage of an individual species' range protected in richness hotspot networks declined as map grid cell size increased. The combined results across all species for each of the four groups evaluated—Arizona birds, Arizona mammals, New Mexico birds, and New Mexico mammals—showed a

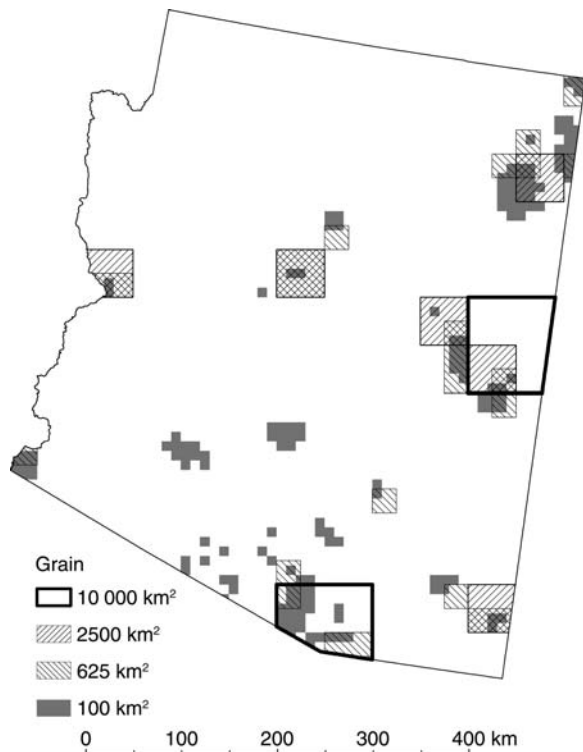


FIG. 4. Spatial overlap of irreplaceability networks for Arizona birds based on four map grains.

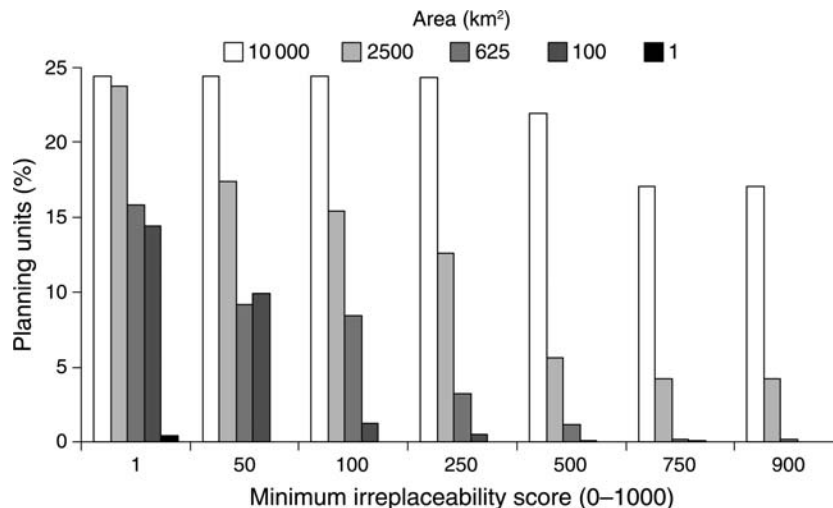


FIG. 5. Irreplaceability of planning units (grid cells) for Arizona bird networks for five map grains. Irreplaceability scores are the number of times a particular planning unit is selected in the best set for each run; e.g., a minimum score of 900 indicates that a planning unit was selected at least 900 times in the 1000 runs.

monotonic decrease from a median of 11.0% range protection in richness hotspot reserve networks created using 1-km² maps to a median of 6.4% range protection in richness hotspot reserve networks created using 10 000-km² maps (Fig. 7). Results for individual groups showed a similar pattern but were more variable, with some finer-grained networks showing lower median percentages of area protected than networks developed at coarser grains. The median range protection for individual species in irreplaceability reserve networks showed a similar pattern of range protection to the richness hotspot reserve networks (Fig. 7). Median percent range protection decreased with increasing grain size with the exception that the 100-km² reserve network showed a lower percent range protection than the 625-km² network.

Global reserve size

In total, we examined records for 8967 terrestrial reserves throughout the globe. Numerous reserves were <1 km² and the largest reserve was 72 000 km². Global reserve size exhibits a positively skewed distribution with a median size of 4.96 km², i.e., 2.23 × 2.23 km (Fig. 8). A significant proportion of reserves are quite small; 31.2% of reserves were <1 km². Very few reserves have been developed at the coarser grain sizes examined in this analysis. Fewer than one in 10 reserves is ≥625 km² and fewer than one in 100 is at least 10 000 km².

DISCUSSION

Scale dependence

The results of this study clearly indicate that conservation planning outcomes are scale dependent, in that reserve networks vary spatially depending on the grain of the data from which they are derived. We found that species richness hotspot reserve networks, best

representation reserve networks, and irreplaceability reserve networks all exhibited low spatial overlap between reserves generated at different map grains (Table 1, Figs. 3–4, Appendix). This lack of spatial coincidence indicates that conservation practitioners must proceed with caution when applying the results of conservation priority setting analyses developed at grains different from those at which identified reserve designs are likely to be implemented. Our results suggest that conservation planners should avoid the uncritical use of coarse-grained data to identify an efficient reserve network which is then used to locate subunits that are actually the units of reserve implementation. This type of strategy is only tenable if fine-grained reserve networks show high degrees of overlap with coarse-grained networks. Our results indicate that this is generally not true.

This study adds to the growing evidence of scale dependence of reserve design outcomes (e.g., Lennon et al. 2001, Warman et al. 2004). While Larsen and Rahbek (2003) conclude that representation networks identified at finer spatial grains are generally nested within those developed at coarser grains, their result is partially due to the tremendous size difference in the reserve networks developed at different grain sizes. The coarsest grain size reserve network they identified included 80% of their study extent, virtually ensuring the nestedness of fine-grained reserve networks. In general, comparison of fine-grained best representation networks to coarse-grained networks is positively biased since the area required to attain full species representation increases as grain size increases (Fig. 2; Larsen and Rahbek 2003, Warman et al. 2004). In our study, the smallest best reserve network was <0.01% of the area of Arizona while the largest was nearly 20% of the state. Despite this difference, we found relatively low (mean, 54.5%)



FIG. 6. Spatial overlap of richness hotspot and irreplaceability reserve networks for Arizona birds generated at four map grains.

spatial overlap between best networks developed at different grains (Fig. 3).

Our analysis of global protected areas showed that most reserves established primarily for biodiversity conservation are relatively small with a median size of 4.96 km². This figure is remarkably similar to the median reserve size of 4.86 km² found by Andelman and Willig (2003) for the Western Hemisphere and highlights the fact that the vast majority of reserves are far smaller than the grain sizes often used to identify reserve networks. A disconnect between the grain of conservation planning and the grain of plan implementation is disconcerting given the low spatial overlap of reserve networks identified at different scales in our study. We found that, worldwide, fewer than 100 terrestrial reserves dedicated strictly to biodiversity conservation are larger than 10,000 km² and that a low percentage of global reserves have been developed at the coarser grain

sizes examined in this study (Fig. 8). Conservation plans are unlikely to be implemented at a large grain and therefore are unlikely to be efficient (Harris et al. 2005). Land availability, parcelization, and development constrain land acquisition, limiting the potential size of reserves. Consequently, efficient conservation planning requires relatively fine scale analyses that approximately match land parcel availability. Therefore, the development of fine-grained species distribution maps for designing reserve networks should be a top priority for conservation planners.

Grain size trade-offs

While data availability may be the key factor dictating the grain of reserve network analyses, conservation planners should carefully consider the trade-offs inherent in using relatively coarse- or fine-grain data (Table 3). The grain of the data used to develop a reserve

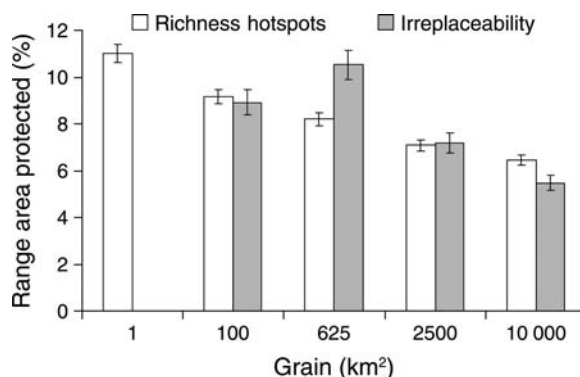


FIG. 7. Percentage of range area protected (median $\pm$ SE) in species richness hotspot and irreplaceability reserve networks. Richness hotspot values represent the means for all individual bird and mammal species. Range area is defined as the total area occupied by a species within a state, not its global distribution area. We did not create a 1-km² irreplaceability reserve network because too few planning units received irreplaceability scores to develop an equal area network at this grain size.

network impacts all aspects of conservation planning including data acquisition and quality, analysis, reserve network properties, and implementation. In addition, conservation goals may change as the grain of planning efforts changes. For example, if a reserve network is designed using fine-grained data, planners may want to impose rules to minimize fragmentation. On the other hand, if coarse-grained data are being used, planners may be more interested in spatial separation of reserves.

Coarse-grained data are much more widely available than fine-grained data and are associated with lower collection costs. In addition, as grain size increases, the probability that a planning unit is actually occupied increases (Williams 1987, 1996), thus improving the likelihood a particular planning unit will provide protection for a targeted species. A further advantage of coarse-grained data is that computer analysis times are reduced. This can be an important factor in reserve selection based on optimizing algorithms such as the MARXAN analysis presented in this paper. On the other hand, coarse-grained data lead to decreased heterogeneity between planning units such that ranking sites is more difficult.

Reserve networks based on coarse-grained data lead to the identification of planning units with large areal extent and therefore benefit from the advantages generally associated with large reserve size if networks are implemented at the same grain at which they are developed. In general, large reserves have increased core areas and decreased edge-to-perimeter ratios and are more likely to maintain ecosystem function and to buffer outside threats (Noss et al. 1997). In addition, area-sensitive species and species that have large home ranges are more likely to persist in larger reserves (Diamond 1975, Gurd et al. 2001). For equal-area reserve networks in which a single population is

preserved within a reserve unit rather than multiple populations in multiple smaller reserves, potential disadvantages of larger reserves are constraints on future evolution (Rubinoff and Powell 2004) and increased vulnerability to disease transmission (Ezenwas 2004).

Fine-grained reserve networks are generally more efficient than coarse-grained networks. For both types of equal area networks that we developed, species richness hotspot and irreplaceability, the number of species represented in networks increased as grain size decreased (Fig. 1). Best representation reserve networks are also more efficient at finer grains due to the dramatic increase in total network area as grain size increases (Fig. 2; Larsen and Rahbek 2003, Warman et al. 2004). The best representation network we developed at a grain size of 10 000 km² was nearly 1000 times larger than the one we developed at 1 km². The inefficiency of the coarse grain is primarily due to the limited degree of species co-occurrence. Two of the planning units in the best 10 000 km² set protect 87% of the species pool (243 of 279 species). The remaining four planning units comprise 43 541 km², which is enough land to create an individual 1210 km² reserve for each of the 36 species unrepresented in the two more speciose planning units.

Our analysis of distribution area protected in reserve networks for individual species showed that, in general, median distribution area protected across individual species decreased as grain size increased for equal area reserves (Fig. 7). Fine-grained reserve networks, especially for species richness hotspots, are more efficient because they protect more distribution area for more species and are therefore more likely to provide long-term persistence. This result may be a function of the fact that large reserve units encompass multiple habitat types such that narrowly distributed or specialist species are unlikely to occupy the entire extent of a reserve unit. In contrast, smaller reserve units are likely to be more homogeneous so individual species are more likely to occupy a relatively larger proportion of each reserve unit. For example, a large planning unit is an inefficient

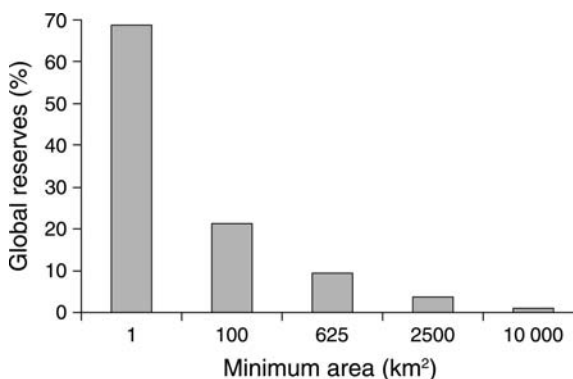


FIG. 8. Percentage of global reserves that are greater than or equal to the area of the five grain sizes used in the richness hotspot and representation reserve network analyses.

TABLE 3. Trade-offs associated with decisions about conservation planning analyses for (a) spatial grain, (b) methodology, and (c) taxonomic representation.

a) Spatial grain	
Coarse grain	Fine grain
Data characteristics	
↑ availability and ↓ collection costs ↑ certainty about actual site occupation	↓ <i>availability and ↑ collection costs</i> ↓ <i>certainty about actual site occupation</i>
Analysis	
↓ computation times ↓ <i>between site heterogeneity leads to ↓ discriminatory power</i>	↑ computation times ↑ between site heterogeneity leads to ↑ discriminatory power
Reserve network properties	
↑ core area, ↓ edge-perimeter ratio ↑ protection of ecosystem function ↑ buffer against outside threats ↑ persistence for area sensitive species ↓ <i>persistence for fragmented or narrowly distributed species</i> ↓ <i>efficiency</i> ↓ <i>genetic variability</i> ↑ <i>vulnerability to disease outbreaks</i>	↓ <i>core area, ↑ edge-perimeter ratio</i> † ↓ <i>protection of ecosystem function</i> † ↓ <i>buffer against outside threats</i> † ↓ <i>persistence for area sensitive species</i> † ↑ persistence for fragmented or narrowly distributed species ↑ efficiency ↑ genetic variability ↓ vulnerability to disease outbreaks
Implementation	
↓ <i>efficiency with analysis grain mismatch</i> ↓ <i>ability to match natural boundaries</i> ↓ <i>ease in plan implementation due to ↑ area requirements/higher costs and ↑ jurisdictions/ownerships</i>	↑ efficiency for consistent analysis grain ↑ ability to match natural boundaries ↑ ease in plan implementation due to ↓ area requirements/lower costs and ↓ jurisdictions/ownerships
b) Methodology	
Hotspot reserves	Representation reserves
↑ mean site diversity Does not prioritize species rare in study extent but widespread elsewhere ↓ <i>species representation</i> ↓ <i>flexibility</i>	↓ <i>mean site diversity</i> <i>May prioritize species rare in study extent but widespread elsewhere</i> ↑ species representation ↑ flexibility
c) Taxonomic representation	
Multi-taxa	Indicator taxa
↑ species representation <i>Impractical due to data limitations</i>	↓ <i>species representation</i> May be only option available

Notes: Up- and down-pointing arrows indicate “increased” and “decreased,” respectively. Attributes that generally have a negative effect on conservation efficiency are shown in italic type. Attributes that are supported by this study are shown in boldface type.

† When sites are not aggregated.

representation of a linear (e.g., riparian) hotspot whereas multiple small planning units will better represent such a hotspot. Because reserve networks are based on underlying species distributions, fine-scale reserve networks are more likely to match distribution boundaries and therefore individual reserves are more likely to be fully occupied by resident species.

Fine-grained reserve networks also offer greater ease of implementation. Land parcel availability is much more likely to match fine-grained planning unit boundaries. Thus, implemented networks can be better matched to the designed reserve and will preserve the efficiencies inherent in the analyses. In addition, land acquisition for smaller reserve units should be facilitated by fewer jurisdictional and ownership boundaries. For best representation networks, the reduced area required for finer grained reserve networks can result in substantial economic savings over coarser grained reserve networks. Ultimately, other issues such as

extinction risk (McCarthy et al. 2005) should also play a role in determining the grain of reserve networks. For example, MARXAN allows the user to impose species specific areal and representation constraints. Incorporating these types of constraints into reserve selection analyses conducted using fine-grain data can ensure persistence for species with large area requirements or high extinction risks while maintaining the efficiencies of using fine-grain data.

Reserve design methodology

We found low spatial overlap between richness hotspot reserve networks and representation reserve networks at each of the spatial grains studied (Fig. 6). Williams et al. (1996) compared richness hotspot reserve networks and representation networks for British birds. Although they did not explicitly consider spatial overlap, their maps show low overlap between the two reserve types. Similar to our results, they found that

richness hotspot reserves were more clustered whereas representation networks were relatively more evenly spread throughout the study extent. In order to include species that occur exclusively in habitats with relatively low species richness, representation networks incorporate a broader spectrum of land types than richness hotspot networks.

Our finding of very low spatial overlap between richness hotspot reserves and irreplaceability reserves emphasizes the importance of carefully considering conservation goals in choosing a reserve design methodology and understanding the trade-offs associated with different methods (Table 3). Richness hotspot networks should be preferred when mean site diversity is an important goal and representation networks should be favored when full representation is a priority (Williams et al. 1996). Potential disadvantages of richness hotspot networks are that some species may remain unprotected and richness hotspots provide little flexibility in implementation. However, planners can attain some flexibility by choosing alternative sites that have slightly lower species richness values, but present fewer acquisition obstacles. Representation networks provide a great deal of flexibility in meeting conservation goals, particularly when reserves are designed using fine-grained data, because many different reserve configurations can achieve comparable representation. Irreplaceability scores show fine-grained analysis provides far more flexibility in selecting specific reserve sites because many sites have similar or identical species composition and are therefore interchangeable (Fig. 5). Although high irreplaceability scores can be interpreted to mean that a particular planning unit has high conservation value, this interpretation is confounded by scale and may be misleading for fine-grained analyses. When multiple fine-grained planning units have similar species composition they receive low irreplaceability scores because the sites are not unique. However, these planning units may be essential to attaining full species representation. Representation networks can be inefficient if they are designed for a relatively small extent because redundancies with reserves outside of the study extent become increasingly likely as the study size decreases (Erasmus et al. 1999). Another potential disadvantage of representation networks is that they can prioritize species that are rare in the study extent, but widespread elsewhere (Erasmus et al. 1999).

While most researchers have studied richness hotspot and representation networks independently, combining the approaches may allow conservation planners to simultaneously achieve these two goals. In our study, species richness hotspot networks contained a high proportion of the species pool. Conservation planners could use hotspots as a starting point for representation networks. Alternatively, species richness could be used as a weighting factor in reserve selection analyses to increase the probability that planning units with

high species richness are included in representation networks.

Taxonomic surrogacy

Comparison of species richness hotspot reserves developed for birds and mammals showed low spatial congruence between the two taxa (Table 2, Appendix). This result held for reserve networks developed for both Arizona and New Mexico at each of the data resolutions investigated and corroborates results found in other studies (e.g., Prendergast et al. 1993, van Jaarsveld et al. 1998; but see Abbitt et al. 2000). Comprehensive taxonomic analysis is undoubtedly the best method for achieving complete species representation and for identifying hotspots; however, data requirements for such analyses are tremendous and currently unavailable in most areas. Using available species as surrogates for all species is usually the only option available. Unfortunately, there is little empirical support that richness hotspot networks and representation networks overlap for diverse taxa.

Conclusions

Conservation planners cannot assume broad scale analyses predict fine-scale results. We found little evidence that coarse-grained reserves designed using either richness or representation criteria subsume reserves designed using fine-grained data. Conservation planners therefore run the risk of designing inefficient reserves if data grains used for reserve analysis are inconsistent with grains for reserve creation. The acquisition of fine-grained species distribution maps or occurrence records is therefore a high priority for effective conservation planning. Furthermore, conservation of richness hotspots and full species representation are both worthy conservation objectives so researchers should focus on developing methods that combine these dual goals.

Low spatial overlap between reserve networks developed at different spatial grains, for different taxa, and using different reserve selection methods indicates that systematic reserve design is not generally robust to spatial grain, taxonomic surrogacy, or methodology. This lack of generality in reserve design schemes suggests that conservation planners must carefully design reserve selection analyses to coincide with stated conservation goals.

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APPENDIX

Richness reserve networks for Arizona and New Mexico birds and mammals developed at five map grains. Maps show spatial overlap of reserve networks developed at different grains and spatial overlap at reserve networks developed for different taxa (*Ecological Archives* A016-057-A1).