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16. Life-history attributes and biodiversity. Scaling implications for global change

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Introduction

Concern with the preservation and management of biological diversity (Soulé 1986) has been amplified by recent speculation about anthropogenic global change (Peters and Darling 1985, Graham 1988, Schneider 1989, Smith and Tirpak 1989). By global change we mean to encompass climatic change--the so-called greenhouse effect--as well as large-scale changes in land use and its associated environmental consequences.

This concern presents two challenges: first, to accelerate the basic process of scientific research toward practical applications, and moreover, to extend or extrapolate our current state of knowledge to scales which ecologists (at least) are not used to managing. These are daunting problems but pressing concerns; we need to move quickly to meet these challenges.

Mechanism and Constraining Context

Biodiversity can be explained in terms of an interplay between life-history mechanisms (the demographic processes of growth, recruitment, and mortality), and environmental constraints (resource availability, disturbance regimes). In a hierarchical perspective, life-history processes are lower-level mechanisms while environmental patterns in resource availability or other boundary conditions are higher-level constraints (Allen and Starr 1982, O'Neill *et al.* 1986, Urban *et al.* 1987). For example, bird population dynamics can be viewed as the consequence of the environmental constraints of food and nest site availability acting on the processes of habitat selection, breeding, dispersal, and mortality of individual birds; larger-scale constraints may include landscape pattern, regional disturbance regimes, and so on (Figure 1).

Scaling problems arise when we attempt to extrapolate information across scales while losing track of important mechanisms or ignoring variability in higher-level constraints. A simple example of such a scaling miscue would be to extrapolate population densities based on a small (ha) censused area to a much larger area (km^2), without correcting for the patchiness of available habitats at the larger scale. Under the specter of global change, these scaling issues could degrade our ability to make valid predictions of the possible consequences of global change on biodiversity.

Here we overview some lessons we have learned about ecological factors governing biodiversity, and the implications of these in scaling up to global concerns. We do this in four vignettes, beginning at a small scale (a forest stand), and proceeding to larger scales (landscape, subcontinental, and global). The vignettes focus initially on forest birds but we believe the lessons are general to conservation practice and biodiversity.

Four Vignettes

1. Microhabitat Pattern and Avian Community Diversity

Microhabitat diversity at the scale of the forest stand (ca. 1-10 ha) is a fundamental constraint on avian community diversity (Urban and Smith 1989). The ecological mechanisms underlying this reflect behavioral aspects of habitat selection by forest birds. James (1971) coined the term "niche gestalt" to refer to the characteristic suite of habitat features (chiefly vegetation structure) associated with the breeding territories of forest songbirds (Figure 2). This concept has underpinned a rich legacy of multivariate statistical studies of habitat relationships (Capen 1981, Verner *et al.* 1986). The variety of such habitat "niches" represented within a forest stand is related directly to the number and variety of birds supported by the stand (MacArthur and MacArthur 1961, MacArthur *et al.* 1962, Roth 1976). The natural pattern of forest development is such that microhabitat diversity tends to increase with time; or, at a given snapshot in time, diversity increases with area (MacArthur and Wilson 1967, Connor and McCoy 1979).

Urban and Smith (1989) used a forest simulation model to illustrate the importance of microhabitat pattern to forest bird communities. They simulated 750 yr of forest dynamics for a 9-ha stand, and summarized microhabitat diversity in terms of the relative abundance of understory versus overstory trees. Bird "species" were defined as random niches (ellipses) in this understory/overstory 2-space, and potential species abundance was estimated in terms the amount of forest habitat falling within the niche space of each species at each time step of the simulation. Simulated community-level patterns in species abundance and diversity corresponded well to patterns observed in real bird communities (Figure 3), which emphasized the fundamental importance of microhabitat pattern to bird community structure.

Phenomenologically, this mechanistic relationship allows one to predict avian diversity as a simple function of stand age (in the time domain) or area (in a spatial domain), so long as the underlying mechanistic relationship holds. Indeed, this relationship is fundamental to the so-called species-area effect (MacArthur and Wilson 1967). "Unnatural" habitat dynamics--such as those mediated by forest management, anthropogenic disturbance, or unusual site conditions--detract from the predictive relationship by degrading the correspondence between stand age (or area) and microhabitat diversity. This is borne out by empirical studies that have shown that measures of habitat diversity can explain variation in avian diversity not explained by forest area (i.e., as significant partial correlations between habitat diversity and bird species diversity: Freemark and Merriam 1986, Lynch and Whigham 1984). The counterpoint to this is the caveat that such predictive relationships cannot be extrapolated to forest stands for which the habitat-area (age) correspondence does not hold. In reality, these invalid cases may be the rule for most habitats in developed landscapes; there are discouragingly few "natural" habitats remaining.

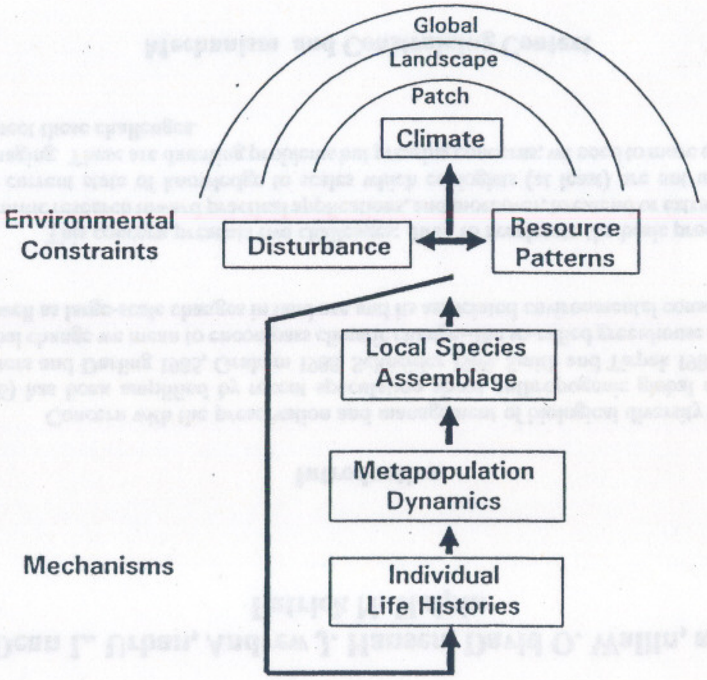


Figure 1. Avian metapopulation dynamics as a consequence of higher-level constraints acting on the demographics of individual birds.

Implications. The scaling lesson here is straightforward. At the scale of the forest stand (habitat patch) there is a mechanistic relationship that can lead to valid and accurate predictions of stand-level biodiversity as a function of stand age or area. But extrapolating such predictions under conditions of environmental change (managed forests, or a change in the relation between habitat structure and resources needed for breeding success) obviates the correlative basis for prediction. Simple extrapolations would be invalid and misleading.

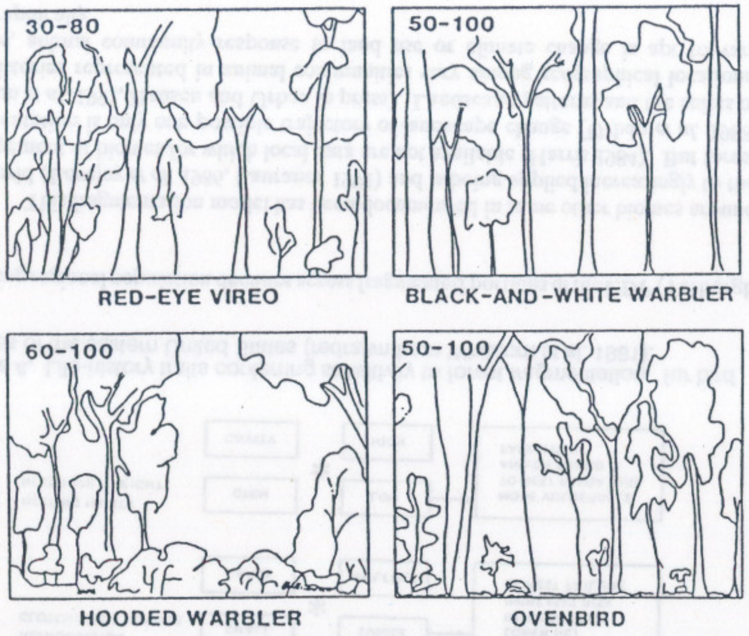


Figure 2. The niche gestalt of birds, as the characteristic vegetation profiles associated with breeding territories (examples redrawn from James 1971).

2. Landscape Pattern and Avian Diversity

As important as microhabitat patterns may be in explaining bird community structure, it has become evident over the past two decades that higher-level phenomena also constrain bird communities. The spatial and temporal patterning of landscapes accounts for additional variation in bird community characteristics. Spatial landscape metrics found to be strongly associated with bird species demography include: size distribution of suitable habitat patches (Forman *et al.* 1976, Ambuel and Temple 1983, Freemark and Merriam 1986, Robbins *et al.* 1989, Laurance 1990); habitat isolation (MacClintock *et al.* 1977, Lynch and Whitcomb 1978, Urban *et al.* 1988); boundary characteristics (Kroodsma 1982, Gates and Gysel 1978, Brittingham and Temple 1983, Wilcove 1985, Harris 1988); patch juxtapositioning (Harris 1984); and habitat diversity (Roth 1976). The effects of change in these metrics over time has been less studied but is likely to be of considerable importance (Franklin and Forman 1987).

The links between bird communities and landscape patterns are best known for forested lands undergoing fragmentation by non forest land uses. Forest fragmentation reduces total forest area, decreases mean patch size, increases the proportion of forest edge, and increases patch isolation (Sharpe *et al.* 1981, Franklin and Forman 1987). Whitcomb *et al.* (1981) identified specific life-history traits that rendered bird species especially vulnerable to forest fragmentation (Figure 4). Many of these species are

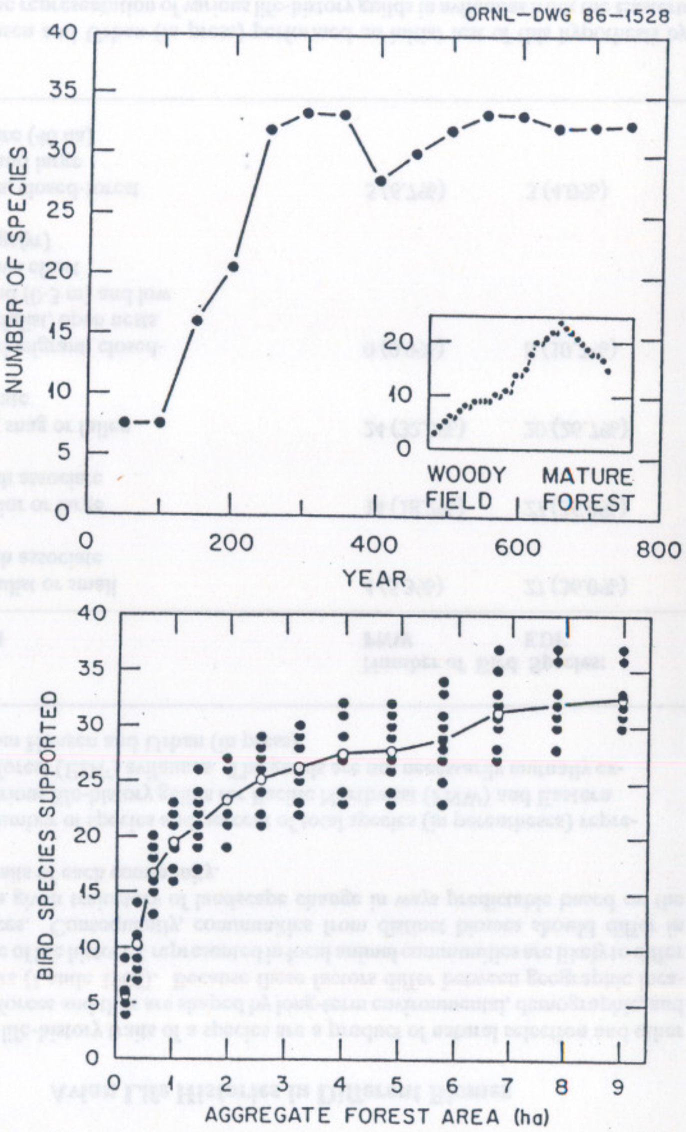


Figure 3. Patterns in forest bird communities as a function of microhabitat dynamics: (a) successional trends in species richness, (b) a species-area effect (from Urban and Smith 1989).

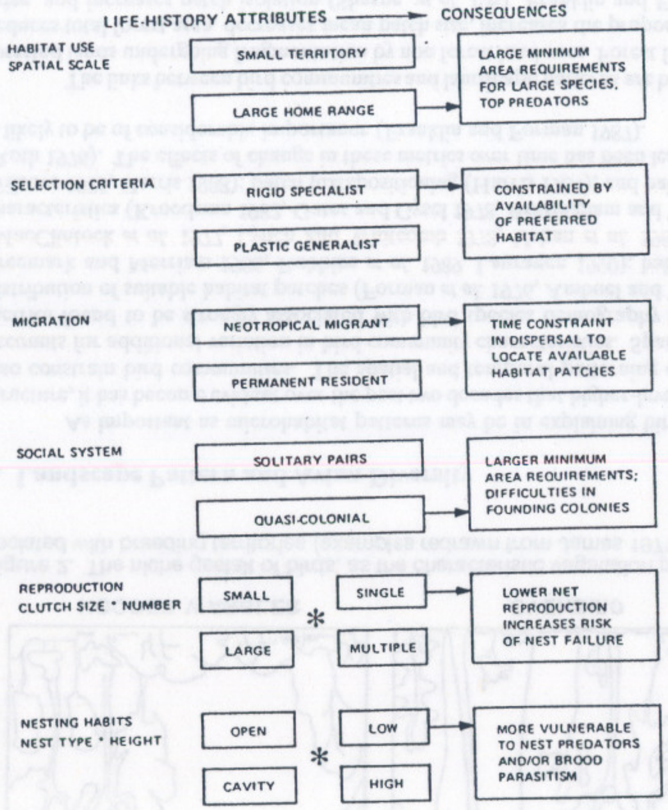


Figure 4. Life-history traits conferring sensitivity to forest fragmentation, for bird species of the eastern United States (redrawn from Whitcom et al. 1981).

suffering regional population declines across fragmented portions of the EDF (Terborgh 1989).

This fragmentation model has been documented in some other biomes around the world (Lovejoy *et al.* 1986, Laurance 1991) and is being applied increasingly to the management of biomes for which local data are not available (Harris 1984). But forest fragmentation is only one possible trajectory of landscape change (Urban *et al.* 1988, Hansen *et al.* 1991, Hansen and Urban in press). Landscape patterns and the suites of life histories represented in animal communities vary among geographical locations. Hence, animal community response to land use or climate change is apt to vary geographically.

In this vignette we summarize studies that compare avian life histories and species sensitivity to landscape change for two biomes. We also contrast bird community dynamics under forest fragmentation with those under two other common trajectories of landscape change.

Avian Life Histories in Different Biomes

The life-history traits of a species are a product of natural selection and other evolutionary forces and thus are shaped by long-term environmental, demographic, and genetic factors (Lande 1982). Because these factors differ between geographic locations, the suite of life histories represented in local animal communities are likely to differ between places. Consequently, communities from distinct biomes should differ in response to a given trajectory of landscape change in ways predictable based on the life-history traits of each community.

Table 1. Number of species and percent of total species (in parentheses) represented in various life-history guilds for Pacific Northwest (PNW) and Eastern Deciduous forest (EDF) avifaunas. The guilds are not necessarily mutually exclusive. From Hansen and Urban (in press).

Guild	Number of Bird Species:	
	PNW	EDF
Edge specialist or small forest patch associate	4 (5.3%)	27 (36.0%)
Patch interior or large forest patch associate	14 (18.7%)	27 (36.0%)
Large tree, snag or fallen tree associate	24 (32.0%)	20 (26.7%)
Neotropical migrant, closed-forest specialist, open nests near ground (0-3 m) and low reproductive effort (< = 6 eggs/yr)	0 (0.0%)	8 (10.7%)
Carnivorous, closed-forest specialist and large territory size (40 ha)	5 (6.7%)	3 (4.0%)

Hansen and Urban (in press) performed an initial test of this hypothesis by comparing the representation of various life-history guilds in avifaunas from the Eastern Deciduous forest (EDF) and Pacific Northwestern (PNW) conifer forests of North America. The EDF avifauna included many more species associated either with forest edges and small habitat patches or with habitat interiors and large habitat patches than did the PNW community; conversely, predators requiring large forest tracts were better represented in the PNW (Table 1). The life-history guild identified by Whitcomb *et al.* (1981) as being highly sensitive to forest fragmentation included eight species in the EDF but none in the PNW.

The relative sensitivity of each community to changing habitat patterns was evaluated by assigning each species a sensitivity index based on its life-history traits. The EDF avifauna in total was found to have a higher index of sensitivity to both forest fragmentation and to landscape change in general (Figure 5).

The validity of using life histories to predict community response to landscape change was supported by the fact that the sensitivity scores for PNW species correlated significantly with independent data on species population trends. As expected, the species most sensitive to landscape change underwent population increases or decreases during this period of dramatic landscape change in the PNW.

This analysis provided evidence that life-history traits are likely to differ among communities and that these differences can cause communities from distinct geographic locations to respond uniquely to a given landscape trajectory. An obvious implication is that conservation strategies should be uniquely tailored to a region based on the types of life-history attributes represented in the community. The challenge in parts of the EDF, for example, is to increase the abundance of forest interior habitats to benefit the large groups of forest-dwelling neotropical migrants. The focus in the PNW should be on maintaining: natural microhabitats, large tracts of forest for forest predators, and sufficiently large openings for open-canopy specialists.

Avian Diversity Under Differing Landscape Trajectories

Because landscape patterns and the environmental constraints imposed by them vary among geographic locations, attention to local landscape patterns is essential to predicting bird community dynamics. Hansen *et al.* (1991) illustrated this point by simulating bird habitat diversity under three common paths of landscape change in human-dominated systems: forest fragmentation, conversion of natural forest to managed plantation, and abandonment of agricultural land (termed *deprise agricole* by the French) (Figure 6). Under forest fragmentation, total forest area was reduced over the course of the simulation; the forest conversion scenario maintained total forest area but converted it to plantations. Under *deprise agricole,* agricultural lands were abandoned over an 80-yr period and then allowed to undergo natural forest dynamics, but with disturbances suppressed. Landscapes simulated under each of these trajectories were classified in term of suitability as habitat for bird species in the PNW avifauna based on four life-history traits (seral stage association, microhabitat requirements, response to forest edges, and territory size). In all cases the model assumed that microhabitat features typical of natural old-growth forest (large trees, snags, fallen trees) were present only in natural stands more than 100 years old, and that these microhabitat features were absent in non forest lands and plantations.

Interestingly, the exercise revealed that even subtle differences in the spatial scaling of landscapes can have strong effects on habitat suitability. Landscape patterns under the forest fragmentation and forest conversion scenarios were similar in that some of the seral stages found in the initial "natural" landscape (natural open-canopy stands and old growth) were lost after only a few decades. The scenarios differed in that total and interior forest area decreased under fragmentation until no forest remained, while forest area remained as high at the end of the conversion to managed forest as in the initial natural landscape.

Under *deprise agricole,* agricultural lands were allowed to gradually undergo forest development over an 80-year period. Thereafter, disturbance was omitted and forest succession resulted in a mixture of mature and old-growth stands after 220 years.

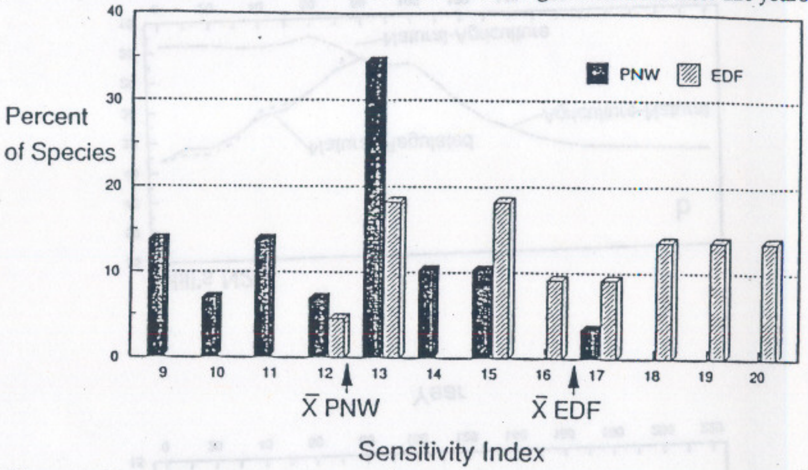


Figure 5. Frequency distributions of scores for sensitivity to forest fragmentation, based on life history-traits, of forest-dwelling bird species from the Pacific Northwest (PNW) and Eastern Deciduous Forest (EDF) avifaunas (from Hansen and Urban, in press).

Some suitable habitat existed in the initial natural landscape for all but 1 of the 51 bird species modeled (Figure 7). Habitats for several species were lost under both forest fragmentation and forest conversion, largely due to the loss of both late seral stages and natural microhabitats. There were important differences, however, in habitat richness between the forest fragmentation and forest conversion scenarios. The abundance of forest cover in the latter maintained habitats for nine more species than did the former. Among these species were some requiring intermediate sized patches of forest interior.

Under *deprise agricole,* habitat richness gradually increased as natural microhabitats and late-successional habitats became available. But habitat diversity in this run did not achieve that of the natural landscape because, under the suppression of natural disturbance, open-canopy and edge habitats were not as abundant as in the natural landscape.

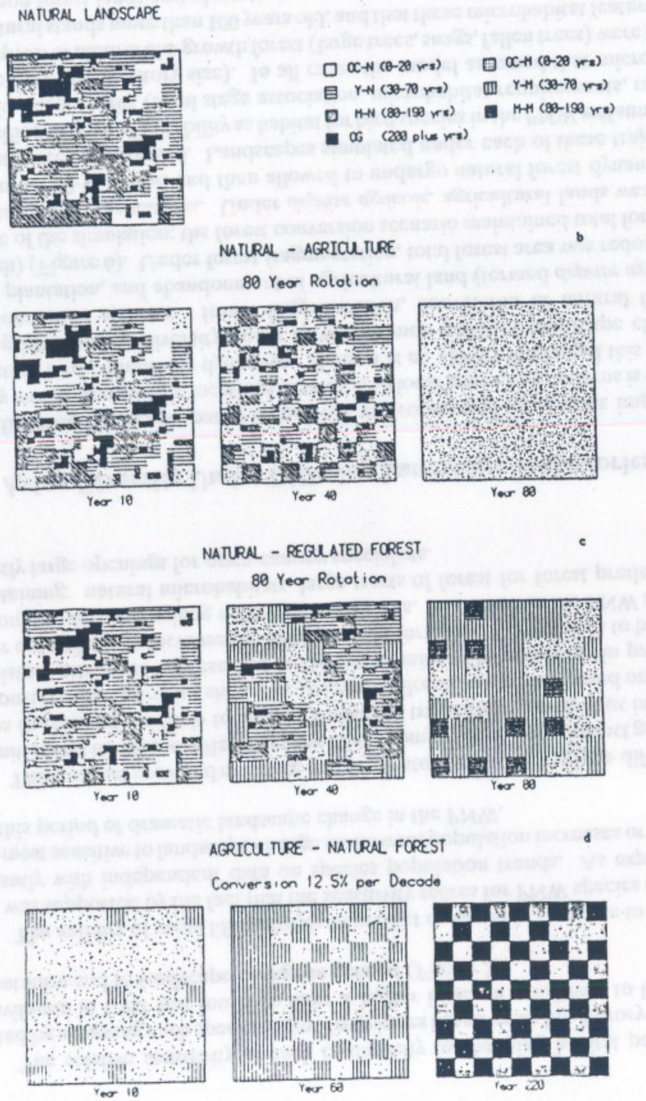


Figure 6. Maps of the simulated landscapes at various time steps. The natural landscape (a) represents year 220 under the fire regime described for a watershed in the Central Oregon Cascade Mountains. The forest fragmentation (b) and conversion to regulated forest (c) runs were initialized with map (a) and subjected to a checkerboard timber harvest regime with an 80-year rotation. The simulation of deprise agricole (d) started as non forest land, underwent forest regeneration for 80 years, forest development continued for 140 years more. From Hansen et al. (1991).

This modeling effort, simple as it was, demonstrated the important role that the type and geometry of habitats across landscapes can play in determining animal community characteristics.

Implications. These studies provide support for the paradigm that local landscape patterns fuel differential responses in animal species according to their individual

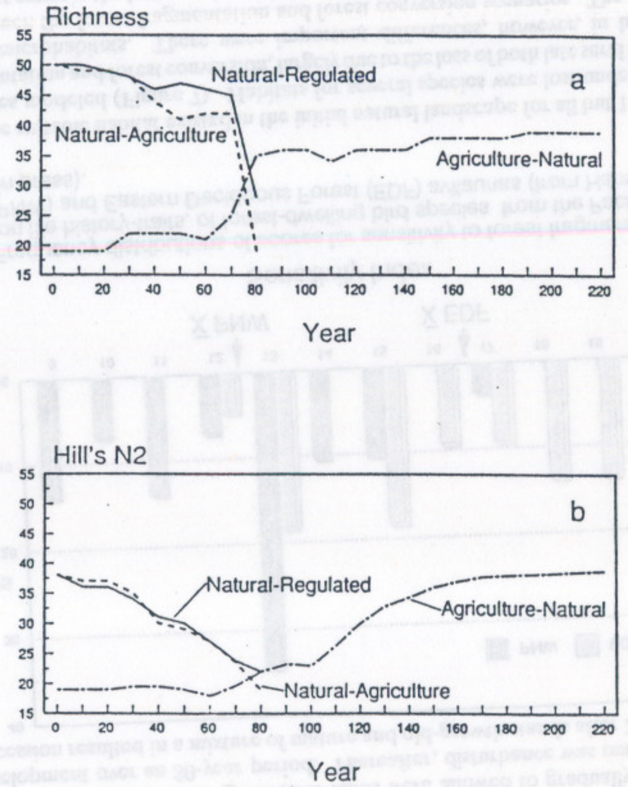


Figure 7. Richness (a) and diversity (b) of habitats for Pacific Northwest bird species over the three simulated landscape trajectories. From Hansen et al. (1991).

life-history strategies, and thus set constraints on the characteristics of animal communities. Both the life-history strategies represented in an avifauna and landscape patterns differ with geographic location. Consequently, it would appear invalid to extrapolate knowledge of animal/landscape relationships to regions or environmental regimes outside the domain of the calibration data. Rather, information on both local landscape context and local explanatory mechanisms are necessary to predict the consequences of land use or climate change.

3. Continental-Scale Patterns and Species Distribution

In this vignette we illustrate how an understanding of the large-scale movement patterns and biogeography of a single species must consider life-history traits and local site phenomena (habitat availability) as well as larger-scale constraints imposed by subcontinental air mass dynamics.

Quelea Life History and Local Patterns. The red-billed quelea (*Quelea quelea*) is a colonial, granivorous weaver-bird (Ploceinae: Ploceidae) found throughout the savannas of sub-Saharan Africa (Ward 1973). Quelea are quite gregarious throughout the year and their dense breeding colonies may often include several hundred thousand pairs and cover a few tens of hectares; colonies in excess of one million pairs are not uncommon (Morel *et al.* 1957, Ward 1965a,b). As a result of its perceived status as an agricultural pest (Bruggers and Elliott 1989, Ward 1979), the red-billed quelea is one of the best studied birds in Africa (Elliott 1979, 1989; Katz 1974, 1976; Ward 1965a; Wiens and Dyer 1977).

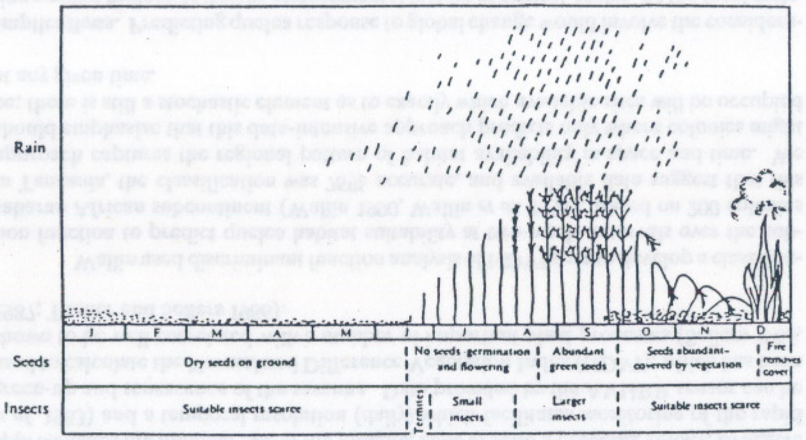


Figure 8. Idealized food availability for Quelea quelea (from Ward 1965a,b,1971).

Quelea feed heavily on grass seeds and also consume insects, particularly during the breeding season. Their diet is generally dominated by a few species of annual grasses (Ward 1965b), which tend to occur in dense stands on clay soils in swales, alluvial fans, and dry lake beds (Ward 1965a, Westoby 1980, Walker 1981). After extended drought and/or under intense grazing pressure, annuals may also dominate other sites for a time (Westoby 1980, Walker 1981). The existence of these stands of annual grasses are thus dependent on a unique disturbance regime which is driven by a combination of factors including rainfall regime, soils, geomorphology and grazing.

The phenology of annual grasses--hence quelea habitat--is driven by seasonal rains, and quelea has a life-history strategy that is geared to these dynamics (Figure 8).

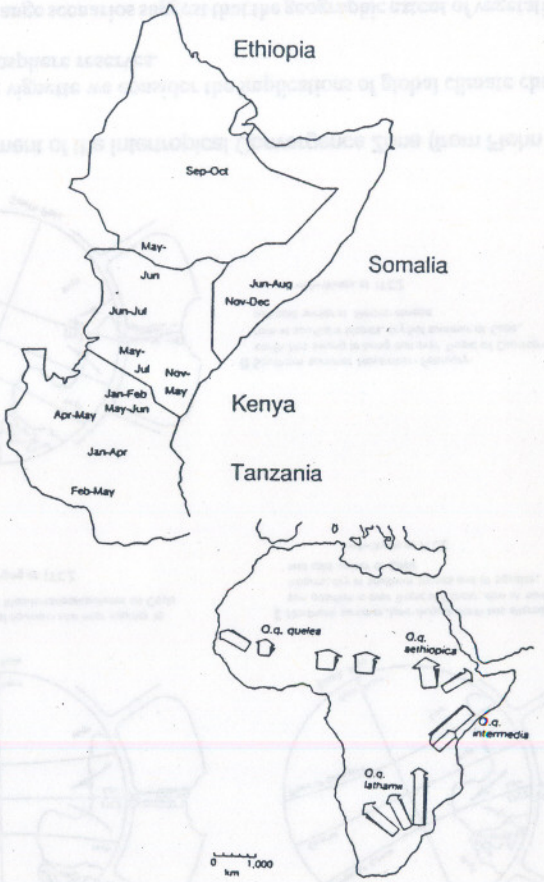


Figure 9. The spatial and temporal distribution of active breeding colonies of Quelea quelea in East Africa, (a) as positions of colonies at dates of known breeding (redrawn from Elliott 1990), and (b) as migration patterns (from Ward 1971).

The entire breeding cycle, from colony initiation to independence of the young, is completed in only six weeks (Ward 1965b; Jones and Ward 1876, 1979). Quelea are highly nomadic (Figure 9). An individual may nest two or possibly three times during a single season at locations which may be tens to hundreds of kilometers apart (Ward 1971, Jaeger *et al.* 1986, Thompson 1988, Elliott 1990, Jones 1990). The nomadic movement patterns, opportunistic nesting and rapid nesting cycle are adaptations which permit the red-billed quelea to exploit this shifting mosaic.

Continental-scale Constraints. On the basis of local observations from a few fixed points on the landscape, the arrival and departure of huge flocks of quelea appear random. A broader overview demonstrates that these movements are driven by large-scale atmospheric circulation patterns. In Africa, the seasonal rains are associated with the passage of an atmospheric circulation feature referred to as the Intertropical Convergence Zone (ITCZ). The ITCZ represents the boundary between northern- and southern-hemisphere air masses and is thus viewed as the meteorological equator (Figure 10).

The ITCZ is a very weak air mass convergence zone. The rainfall produced within the ITCZ is convective in origin, occurs in relatively small (1-2 km^2) patches, and its distribution is highly unpredictable both within and between years. The convective rainfall cells embedded within the ITCZ and the seasonal movement of the ITCZ over the African continent produce the shifting mosaic of resource patches which force the red-billed quelea to move across the landscape.

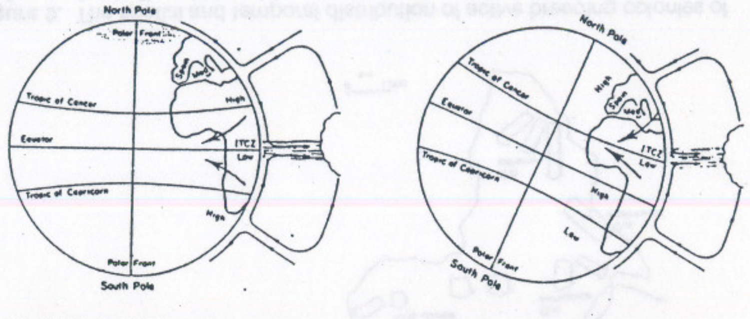
A dynamic regional overview of breeding habitat availability for the red-billed quelea can be obtained by directly monitoring vegetation dynamics using coarse-resolution satellite data (Wallin 1990, Wallin *et al.* 1991). Data provided by the Advanced Very High Resolution Radiometer (AVHRR) have a suitable spatial resolution (4 km, which approximates the minimal size of the foraging zone around a breeding colony, Bruggers *et al.* 1983) and a temporal resolution (daily) which facilitates monitoring of the rapid green-up and senescence of the savanna. Data provided by the AVHRR sensor can be used to calculate the Normalized Difference Vegetation Index (NDVI), which has been shown to be well correlated with a number of important plant processes (Sellers 1985, 1987; Tucker and Sellers 1986).

Wallin used discriminant function analysis of NDVI data to develop a classification function to predict quelea habitat suitability at two-week intervals over the sub-saharan African subcontinent (Wallin 1990, Wallin *et al.* 1991). Based on 200 colonies in Tanzania, the classification was 76% accurate, and available data suggest that this approach captures the regional pattern of habitat availability in space and time. We should emphasize that this data-intensive approach predicts only where colonies might be; there is still a stochastic element as to exactly which available sites will be occupied at any given time.

Implications. Predicting quelea response to global change would involve the consideration species biology as well as environmental factors at several scales. At the local scale, an increase in the reliability of rainfall may result in an increase in the amount of perennial grasses and a decrease in the annual grasses upon which quelea depend. More reliable rainfall could also result in an increase in the populations of resident predators or granivorous competitors. A decrease in the duration of the rains could decrease the window of opportunity for nesting to the extent that quelea would no longer able to complete their nesting cycle. Finally, changes in grazing pressure keyed on altered grassland dynamics could also have an impact on quelea habitat. While it is feasible to attend these relationships in sufficient detail to make predictions at the subcontinental scale, such an approach is logistically daunting and very data-intensive.

4. Biosphere Reserves and Global Change

Our first three vignettes suggest that species life-history traits interact with environmental constraints at multiple scales (local, landscape, and continental) to generate patterns in species abundance and diversity. How, then, do we reconcile the richness of these relationships to a concern for global biodiversity? Clearly, the approach we have illustrated thus far would be logistically overwhelming if extended to many species and large scales. An alternative is the coarse-filter approach (Hunter *et al.* 1988), wherein representative samples of ecosystems are maintained in the hope that their internal diversity will be preserved as well. This is the basis for biosphere reserve systems. In this last vignette we consider the implications of global climate change to a static network of biosphere reserves.

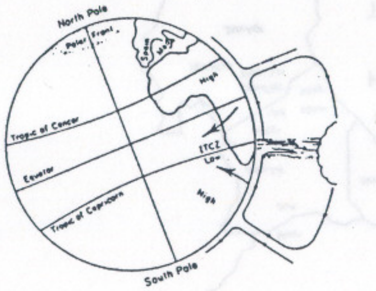


I At vernal and autumnal equinox: rain near equator to about 4° N-S; spring in Mediterranean; autumn at Cape

←Winds converging at ITCZ

II Northern summer June-August earth has altered position till sun position is over Tropic of Cancer; rain in northern tropics; dry in southern tropics and at equator; wet cold winter at Cape

←Winds at ITCZ



III Southern summer November-February: earth has swung to bring sun over Tropic of Capricorn; rain in southern tropics; dry hot summer at Cape, wet cold winter in Mediterranean

←Winds at ITCZ

Figure 10. Movement of the Intertropical Convergence Zone (from Flohn 1987).

Climate-change scenarios suggest that the geographic extent of vegetation types might shift through the stationary boundaries of established nature reserves. This translocation of vegetation ranges could act to further fragment vestiges of protected species habitat. Local extinctions of reserve species occur through either direct physiological reactions of species to changed climatic conditions or through changes in interspecies competition due to alterations in the composition of species across the landscape (Figure 11) (Peters and Darling 1985, Noss 1987, Hunter et al. 1988).

Predicting the potential effects of climatic shifts on reserve systems requires a geographically referenced vegetation model which can be manipulated directly to represent the potential impacts expected from different climate-change scenarios. Coarse-resolution associations between vegetation zones or biotic provinces and climatic patterns are well established in ecology. Assuming that extant vegetation is more-or-less at equilibrium with current climate, correlative models of climate-vegetation associations can be developed (Holdridge 1967, Box 1981). From these types of models, potential shifts in vegetation pattern can be projected from general circulation model (GCM) experiments conducted by climatological research groups (Emanuel *et al.* 1985, Shugart 1990, Smith et al. 1990).

One such approach has involved the development of a global climate data base which can be used to calculate the spatial distribution of major ecoclimatic types (biotic provinces or biomes) and then track potential changes in the distribution of these types due to various climate-change scenarios. The model includes current climate parameters for a 0.5° x 0.5° latitude and longitude grid (Emanuel *et al.* 1985, Leemans and Cramer 1990, Smith *et al.* 1990). The climatic data from this grid were then used to predict ecoclimatic regions using the Holdridge life-zone approach (Holdridge 1967). The Holdridge classification system is a correlative ecoclimatic model which relates general vegetation associations to indices of biotemperature and precipitation. The simplicity of the Holdridge method makes this approach very straightforward to use in conjunction with the output from global circulation models, for projecting large-scale shifts in vegetation patterns expected from climatic change.

Climate-change scenarios derived from four general circulation models were used to alter the baseline climatic grid to predict the expected equilibrium vegetation conditions projected under climate change. All four scenarios produced significant shifts in major biome types on a global scale (Table 2) (Smith *et al.* 1990, Monserud 1990). A large proportion of these changes were in northern latitudes, reflecting the greater temperature increases predicted in these regions.

As a first assessment of the potential impacts of climate change on a global system of nature reserves, a distribution of Man and the Biosphere (MAB) reserve sites was geo-referenced into the global grid vegetation model. Halpin and Smith, in prep.; Smith *et al.* 1990). Each reserve was assigned a present Holdridge life zone classification, with changes in life zone occurring as a result of the climatic changes predicted from the four GCM scenarios recorded as potential impacts.

The four scenarios could have a significant impact on global reserve systems (Figure 12). From a global perspective, a comparison of the percent of reserves impacted to the total area of terrestrial life zone change for each GCM scenario reveals a significant bias in impacts of MAB reserves relative to total global vegetation change. The numbers of reserves impacted by climatic change is from 12% (OSU) to 30% (UKMO) higher than the amount of total vegetation change calculated for each scenario. This bias is most likely attributable to the non uniform distribution of global reserves. A disproportionate number of reserves in the MAB system are located in the northern latitudes, specifically in Europe and North America. This geographic bias of established reserve systems to the more developed countries of the northern hemisphere puts a larger numerical distribution of reserves in regions which experience a greater magnitude of climatic change under all scenarios (Halpin and Smith, in prep.).

In general, global-scale analysis of the potential impacts of anthropogenic climate change on nature reserves offers insights into the general distribution of impacts and identifies those types suffering the highest potential loss of protection (Halpin and Smith, in prep.). On the other hand, global-scale analysis fails to offer detailed information distinguishing potential impacts within reserve areas and smaller management regions. The analysis also sacrifices the details of relationships more subtle than the simple correlative climate-vegetation model.

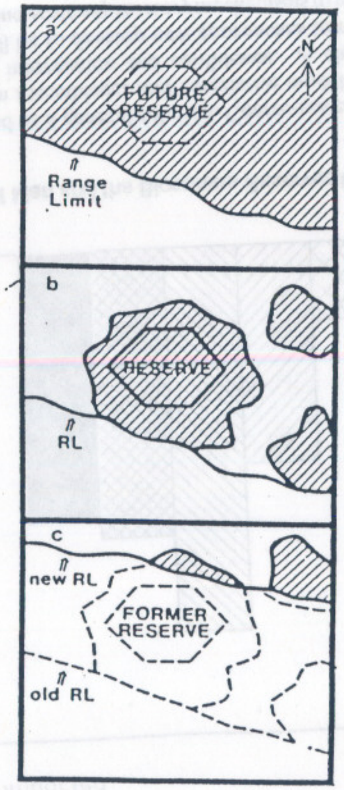


Figure 11. Potential effects of shifting climatic ranges on species occupation of a hypothetical nature reserve: (a) original species distribution; (b) species distribution after human fragmentation of the landscape; (c) species distribution after climatic shift (from Peters and Darling 1985).

Table 2. Percentage of terrestrial land area showing a shift in life zone under changed climate (from Smith *et al.* 1990).

Scenario[1]	Percent of Land Area Changed
GFDL	48.0
GISS	44.3
OSU	39.4
UKMO	55.0

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[1] Scenarios are 2x CO_2 climate-change scenarios provided by the following general circulation models: Geophysical Fluid Dynamics Lab (GFDL), Goddard Institute of Space Studies (GISS), Oregon State University (OSU), and United Kingdom Met Office (UKMO); all as provided by the U.S. Environmental Protection Agency (with no liability or endorsement implied).

Implications. Interpreting the potential impacts of climate change for nature reserves poses some unique problems. Some reserves are selected because they represent archetypal examples of the general ecological region in which they are located; on the other hand, some are selected for the opposite reason: because they represent atypical associations of species or relics of past climates. These alternative criteria in reserve selection become problematic when using coarse-resolution global-scale models, which average climate and vegetation characteristics over large spatial areas. Such models fail to distinguish the current characteristics of unusual habitats (Halpin and Smith, in prep.), and thus cannot be used confidently to project vegetation response to environmental change.

Conclusions

In closing, we should emphasize the power of life-history mechanisms and constraining context as explanatory principles at whatever scale. So long as these hold up, simple correlative relationships can be derived to provide valid predictions about biodiversity patterns in space or time. If either the mechanisms or the constraints are changed, correlative predictions may no longer be valid.

Extrapolating from one system to another can lead to confusion or misleading predictions if the systems differ in their mechanisms or context. This can be a real danger in global-change research, since we are constantly on the edge of our knowledge base and limited by available data.

At increasingly larger scales, and especially at the global scale, we come to a dichotomy in possible approaches to managing biodiversity. A mechanistic approach based on life-history traits and environmental constraints can provide a powerful predictive model, which may be applied from local to regional scales. Beyond this scale, the details of this approach become logistically daunting. This approach might still be recommended for certain well-studied focal species (e.g., endangered species) but it cannot be recommended as a general solution. Coarse-scale approaches based on life forms or type vegetation assemblages and correlative models can be applied at larger scales, at some loss of information and confidence. A challenge to researchers in conservation biology will be to develop new approaches to reconciling information at multiple scales, linking fine-scale explanatory mechanisms to global patterns in biodiversity.

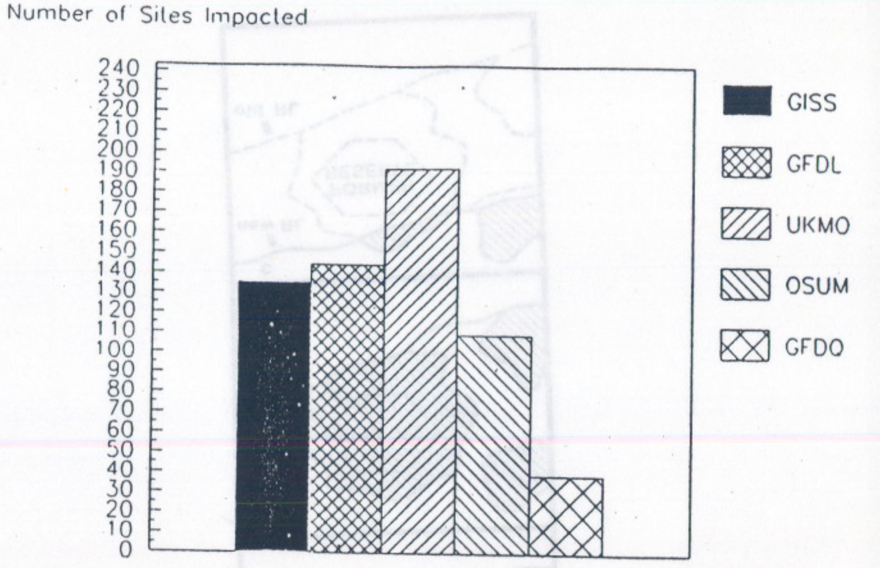

Figure 12. Percent of Man and the Biosphere Reserves Impacted under climate change scenarios.

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