BIRD DIVERSITY COMPONENTS IN AUSTRALIAN *EUCALYPTUS* AND NORTH-TEMPERATE *QUERCUS* WOODLANDS

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ABSTRACT.—Diversity patterns of breeding bird assemblages (exclusive of raptors and nocturnal species) of western North American oak and Australian eucalypt woodlands are derived from data recorded at 113 census sites distributed over four regions, two on each continent. Regional species richness varies by a factor of 2 among regions. The contribution to regional species totals by various diversity components is examined: α-diversity (species richness within sites), β-diversity (species turnover between sites related to differences in vegetation structure), and γ-diversity (turnover related to distance between sites, independent of habitat change). Mean α-diversity is relatively constant among regions (mean 25.5 to 29.7 species). Variation in α-diversity within regions is related to variation in vegetation structure, and bird-density variation is best predicted by a measure of vegetation density. The relationships between bird diversity and density and vegetation structure are similar in the four regions. With the influence of vegetation structure removed, there is no (Australia) or at best a modest (North America) latitudinal gradient in α-diversity. Within regions, regression analysis shows that species turnover is significantly related to both vegetation structural differences (β-diversity) and distance between sites (γ-diversity), with the latter accounting for a larger proportion of, and correlating strongly with, regional species totals. Identification of factors promoting species turnover between sites, beyond distance and vegetation effects, remains a major challenge to ecologists. *Received 23 September 1999, accepted 13 December 2000.*

PATTERNS OF SPECIES RICHNESS have attracted ecologists for many decades. Description of these patterns and explanations for some aspects of their origins are found in books (Ricklefs and Schluter 1993, Rozensweig 1995, Brown and Lomolino 1998) as well as in a burgeoning primary literature. Earlier work emphasized "ecological" and "equilibrial" aspects of the problem, for example, prediction of species numbers from structural characteristics of the habitat (MacArthur and MacArthur 1961, Pianka 1966a, Sheldon 1968) and possible explanations for latitudinal diversity gradients (Pianka 1966b, Terborgh 1973). More recently, the literature has emphasized both a closer examination of spatial scale and complexity (Monkkonen 1994, Bohning-Gaese 1997, Davidowitz and Rozensweig 1998, Stillman and Brown 1998) and a larger role for history, chance, and divergent evolutionary pathways between geographical regions (Ricklefs and Schluter 1993 and many contributions therein). Clearly a multitude of factors, operating over a wide range of temporal and spatial scales, is responsible for the generation and

maintenance of species-diversity patterns, and comparative studies at broader geographical scales (e.g. intercontinental) seem particularly productive (e.g. Monkkonen 1994) but are rather uncommon.

Regional patterns of species richness, such as number of lizard species in Amazonia, number of land snails in North America, or number of bird species in South African shrublands, may be best understood in terms of diversity components (Cody 1975, 1983, 1986, 1993). Regional species totals can be partitioned into components that reflect (1) numbers of species co-occurring at a single site of homogeneous habitat, or α-diversity; (2) accrual rate of new species as sites are censused over a range of habitat variation, or β-diversity; and (3) addition of new species to the regional total as more distant sites, but within the same habitats, are assessed, a γ-diversity component. In general terms, α-diversity measures the extent to which species coexist in local communities by dint of resource partitioning via diversified adaptations, β-diversity quantifies the degree to which structural or other variation in habitat promotes a species turnover or replacement between sites, and γ-diversity represents the ex-

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tent to which ecological counterparts are sub-stituted in different parts of a habitat's range. Note that my definition of γ-diversity is differ-ent from that originally proposed by Whittaker (1972) and repeated by Brown and Lomolino (1998) as a loose measure of "landscape diver-sity." That latter is equivalent to a regional spe-cies total S_T, and I define γ-diversity as a quan-tifiable, distance-related component of this regional total.

Consideration of diversity components facil-itates not only a description of patterns, but also an understanding of processes that lead to their evolution. Thence, comparisons of diver-sity components within taxa (e.g. plants, snakes, birds) among regions (e.g. North Amer-ica, South Africa, Australia) may greatly aid in the identification of factors that enhance or per-haps limit development of a particular com-ponent of diversity, in the same way that inter-continental comparisons of (unrelated) taxa at species level lead to better understanding of adaptations that promote or constrain conver-gent evolution.

Here I adopt a comparative approach to an evaluation of bird species diversity in Northern Hemisphere oak (*Quercus* spp.) and Southern Hemisphere eucalypt (*Eucalyptus* spp.) wood-lands, and contrast census data within and among different regions of North America and Australia. The comparison makes use of some strong parallels between oak and eucalypt woodlands: (1) both genera include species that dominate canopy vegetation at diverse sites over wide latitudinal ranges in their respective hemispheres; (2) species richness in both gen-era is high, with ~450 species of Australian *Eu-calyptus* and 240 species of North American *Quercus*; (3) species in both genera may be ev-ergreen, or deciduous (e.g. at higher latitudes, elevations, or in the seasonal tropics), or some-what intermediate; and (4) both include species that collectively span a range of growth forms from tall trees to low, multistemmed shrubs. Thus, there is a degree of floristic uniformity within regions, and a case for ecological equiv-alence of the habitat dominants between re-gions and hemispheres.

In this paper, I compare diversity, density, and species composition of bird communities of a wide variety of Australian eucalypt and North American oak woodlands. Breeding bird census data are synthesized from 113 sites, at 97 of which measures of vegetation structure also were made. Those data are used to deter-mine patterns of bird species diversity and its components, of bird density and its variation, and of species turnover rates with changing vegetation and with the geographical separa-tion of sites. Further, those *Eucalyptus* and *Quercus* woodlands are useful for examining latitudinal trends in diversity while controlling for plant dominants in the vegetation (e.g. Keast et al. 1985). Although aspects of vegeta-tion structure were shown previously to con-tribute significantly to predictions of α-diver-sity in eucalypt woodlands (Cody 1994a), there is no significant effect of latitude (over a 20° range) in Australia; the same has been shown true of other Australian habitats such as heath-lands (Cody 1994b) and mulga (Cody 1994c). In contrast, latitudinal effects are more pro-nounced for birds in the North American oak habitats. Indistinct latitudinal gradients in α-diversity may be partly attributable to con-trolled floristics (i.e. the dominant plant genera are constant) and to the fact that both oak and eucalypt woodlands occupy strongly seasonal sites at low latitudes.

STUDY AREAS AND METHODS

Habitats and floristics.—The habitats employed in this study are loosely classified as woodlands, in which canopy cover is discontinuous and generally in the range 40–75% (Specht 1973). Vegetation height reaches 30 m at some sites, but is much lower (down to ~5 m) at others where the dominant plants are shrubby oaks or mallee eucalypts. Sites are restricted to habitats in which the oak or eucalypt dominants constitute ≥2/3 of the total canopy cover. In each re-gion, sites may have a single dominant oak or eu-calyptus species, but more commonly there are sev-eral codominants. At several more southerly North American sites, conifers constitute a component of the vegetation, especially junipers (*Juniperus* spp.) and pines (*Pinus* spp.); in more arid Australian sites, conifer-like *Casuarina* spp. play a similar role.

Study sites by region.—Study sites are divided into four regions on two continents (see Table 1 and Fig. 1) as follows: (1) CA (California, including sites along the Pacific coastal area west of the Sierra Ne-vada and Cascade Mountains from Washington State to the Cape region of Baja California); (2) ACM (Ar-izona–Colorado–Mexico), from the southern Rocky Mountains (Colorado) south through the Sierra Ma-dre Occidental (northwest Mexico) to the Sierra Ma-dre del Sur, southern Mexico; (3) QLD (Queensland, Australia, from Cape York south to the New South

TABLE 1. Data set characteristics for four regions, on the two continents. See text for explanation of abbreviations.

Region site # (MLC sites)	S_T	S_J + 95% CI	Lat. Range	Long. Range	Veg. ht.	Prof. area	#SPP (α-divers.)	Density (pr/ha)
					(Mean ± SD, range)		Mean ± SD	Mean ± SD
CA	112	138.3	23.5°	110.0°	15.2 ± 5.1 m	34.8 ± 8.2	27.7	10.7
n = 40		± 14.2	46.8°	−123.0°	3.6–21.8	15.3–46.8	±7.1	±4.1
(30)								
ACM	166	214.9	19.5°	103.1°	14.9 ± 8.1 m	22.0 ± 6.6	29.7	8.7
n = 24		± 20.2	−31.9°	−109.2°	4.8–31.2	12.0–32.8	±8.2	±5.1
(17)								
QLD	155	190.8	11.7°	142.6°	12.8 ± 3.1 m	19.8 ± 6.9	27.2	7.3
n = 32		± 15.0	−30.6°	−153.1°	7.1–20.2	8.2–39.8	±7.8	±2.7
(32)								
WA	88	103.1	27.7°	114.7°	14.3 ± 3.5 m	16.8 ± 5.8	25.5	5.8
n = 17		10.7	−33.8°	−123.8°	7.1–23.0	7.7–33.5	±6.2	±2.0
(17)								

Wales border); and (4) WA (southwest Western Australia. Three of those regions span latitudinal ranges of 20° or more (Fig. 1). The two North American woodland regions are separated by habitat barriers of largely treeless deserts (Sonoran, Mojave, Great Basin). The woodlands of southwest Australia are isolated from similar habitat north and east by interior deserts of *Triodia* grassland and intermittent shrublands, which reach the west coast at Shark Bay and the south coast on the Nullarbor Plain.

The number of sites at which bird and vegetation data were collected varies among regions, from 17 (WA) to 32 (QLD). The North American database is supplemented by a number of published censuses

(17 other than my own) for most of which there are census results, but no comparable measurements of vegetation (see Table 1; CA [40 sites; 30 with vegetation data], ACM [24; 17]); a total of 113 sites contributes to α-diversity comparisons, 97 to comparisons involving vegetation measurements.

Reference has been made to oak and eucalyptus bird communities in a number of previous publications: for CA oak woodlands (Cody 1974, 1999), ACM woodlands (Cody 1974, 1981), and eucalyptus woodlands in Australia (Cody 1986, 1993, 1994a). This paper attempts to generate an overview of diversity patterns from this broad database by means of regional and intercontinental perspectives.

Bird census protocols.—Censuses were made of bird communities within the breeding season, which is April–June at north-temperate sites and September–November at Australian sites. Data were gathered at most CA sites in spring 1994, at ACM sites over several seasons from 1979 to 1982, and in (austral) spring 1984 in WA and 1989 in QLD. Census sites ~5 ha in size were chosen and mapped and situated to the extent possible in relatively homogeneous habitat to avoid edge effects. At least three visits were made to each site; two of these were early morning visits. The number of breeding pairs of each resident bird species was counted, using sight and sound records, and incorporated with spot-mapping techniques into the site map. Raptors and nocturnal species were excluded from counts.

From census data, number of bird species breeding or regularly foraging within the study sites was computed, together with density (pairs per hectare) of each species. For species with territories only partially within the census site, territory extent beyond the study site was observed and evaluated and the proportion of the territory within the site estimated. For the several Australian species that occupied group territories, density estimates were made from
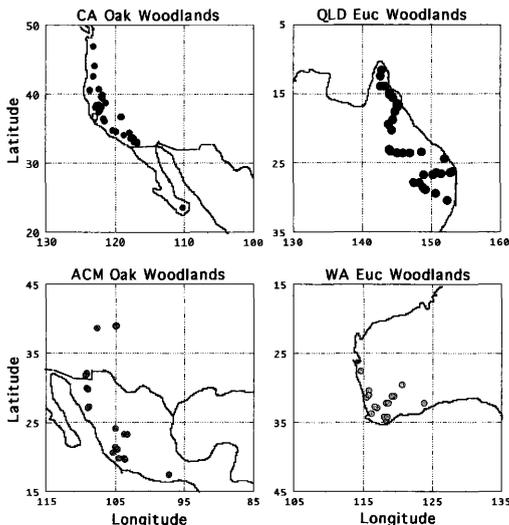

FIG. 1. Geographical distribution of 113 bird census sites in oak woodlands (North America: two regions, left) and eucalyptus woodlands (Australia: two regions, right).

counts of adult individuals per hectare, and incorporated into overall density figures of pairs per hectare by dividing by two.

Vegetation measurements.—At each census site, a vegetation profile was constructed by plotting vegetation density (abscissa) versus height above ground (ordinate). Vegetation density was derived from estimates of horizontal distances at which an imaginary board is half-obscured from the observer by vegetation, in four orthogonal directions at each of five randomly selected points within the site ($n = 20$). Distance to half-obscurity was estimated at standard heights above ground: 0.15, 0.3, 0.6, 1.2, 2, 3, 4.5, 6, 7.5, 10, 15, 20, 25, and 30 m. Estimation of those distances at heights well above ground level is facilitated by the relative openness of the vegetation and enhanced for comparative purposes by observer practice and constancy. Reciprocals of those distances were averaged to give the site profile, which is a plot of vegetation density as a function of height above ground. Three derivatives of the profile were used as summary vegetation statistics: profile area (AR: area under the profile in units of 0.3 m [ordinate] by (3 m)$^{-1}$ [abscissa]), vegetation height (HT) above which horizontal distance to semiobscurity exceeds (by convention) 30 m, and vegetation "half-height" (HHT), a median level at which half the profile area lies below and half above.

Data reduction.—Within regions, census sites collectively yield a total (regional) species number S_T. Regional species totals are compared in several ways: (1) by contrasting S_T values or (2) jackknife estimates of S_T based on the number of unique species k in the n census lists: $S_J = S_T + (n + 1)k/n$ (Heltshe and Forrester 1983), and (3) by bootstrap simulation of cumulative species censused in random subsets of the censuses taken 2, 3, 5, 7, 10, or more at a time. Species ($CUMSPP$) are accumulated as an increasing function of number of censuses ($SAMPLE$) in the subset; the simulation data are fitted to the curve $CUMSPP = A \times (1\text{-}B \times e^{(-C \times SAMPLE)})$ and its parameters derived by least-squares regression and estimated with 95% confidence limits. In particular, the asymptote A can be compared among regions for a fixed number of censuses, for example, $ASYMPT10$ for random samples of 10 censuses per region.

Each census site yields a measure of α-diversity, number of breeding species (SPP), and total breeding bird density in pairs per hectare ($DENS$). Each of those measures was related to geographical position (latitude, LAT) and measures of vegetation structure (AR, HT, HHT). Effects of vegetation structure on SPP and $DENS$ were tested by linear regression, and the residuals from those plots used as dependent variables in linear regressions with latitude.

The CA oak woodland censuses are used to evaluate the extent to which species are accumulated at a given site with varying numbers of replicated samples in different years, and the extent to which censuses differ within sites between years as a function of the intercensus interval. The published censuses (above; Table 1) together with my repeat censuses of some of those sites are used chiefly for this purpose.

Census data within regions are compared in terms of (1) bird species turnover between paired sites ($SPTURN$), computed using the formula $100 \times (1 - c \times (T_1 + T_2)/(2 \times T_1 T_2))$, where the two paired sites support T_1 and T_2 breeding species respectively and share c species in common (Cody 1993; see Krebs 1999 for a discussion of alternative indices). The same paired sites also yield (2) a measure of difference in vegetation structure ($VGTURN$), measured as $((\log HT_1 - \log HT_2)^2 + (\log AR_1 - \log AR_2)^2)^{0.5}$, and (3) site separation distance ($DIST$), which is approximated from site latitude (LAT) and longitude (LON) coordinates, to two decimal places, as $0.1 \times ((LAT_1 - LAT_2)^2 + (LON_1 - LON_2)^2)^{0.5}$, with units of 10^3 km.

Comparisons among regional species totals, site species counts, and vegetation measures are made by ANOVA with Bonferroni corrections. As effects of $VGTURN$ and $DIST$ on $SPTURN$ involve multiple comparisons, multiple full and partial regression coefficients and full and partial correlation coefficients were computed using partial Mantel techniques (Mantel 1967, Smouse et al. 1986). Significance tests for Mantel statistics were conducted by computing all regression and correlation coefficients from 100 randomized versions of the dependent variable matrix ($SPTURN$ values), in which each element is drawn at random from a normal distribution with the mean and standard deviation of the observed $SPTURN$ values. That randomization procedure makes use of the fact that $SPTURN$ is in all cases normally distributed (Lilliefors test for normality). All statistical analyses, tests and simulations were carried out in version 5.2.1 of SYSTAT™ (Systat 1992).

RESULTS

Comparisons of vegetation structure.—Vegetation structure at 97 study sites is generally similar among regions (Fig. 2, Table 1), but there are some differences. ANOVA with Bonferroni corrections shows that vegetation height HT does not differ significantly among regions ($P > 0.05$), but overall vegetation density AR is significantly higher in CA than in the other three regions ($P < 0.01$). That may reflect the influence of the Mediterranean-type climate in coastal California, although vegetation density in oak woodlands may vary at sites among years due to short-term weather variation (e.g. at the Chiricahua Mountains, Arizona, site; Cody 1981).

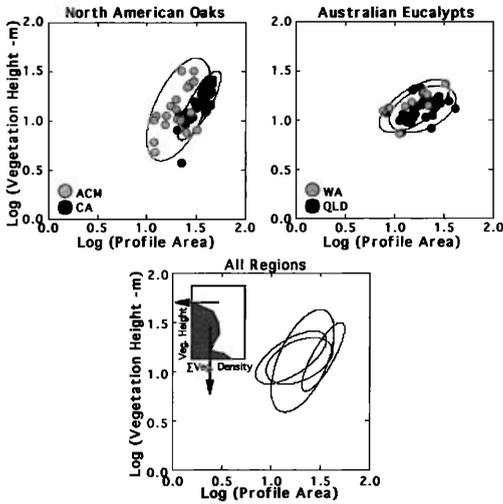*Regional species diversity.*—The total number of bird species censused within regions (S_T)

FIG. 2. Comparative vegetation structure of census sites in four census regions. Axes are summary variables derived from vegetation profile (see lower figure, inset) at each site; data points for each region are bounded by a 95% confidence ellipse. Vegetation is generally similar among regions (lower figure), but vegetation in Californian oaks is more dense, producing somewhat larger profile areas.

varies from 88 (WA) to 166 (ACM). Jackknife estimates of regional species totals (Table 1, Fig. 3) inflate S_T by an additional 17% (WA) to 29% (ACM), versus 23% in CA and QLD. Bootstrap simulations of cumulative species as a function of number of census sites show distinct differences among regions (Fig. 3), with the species accumulation curve fitted to the full data set. As the number of census sites varies among regions (from 17–32), I compare regions in terms of equal samples of site numbers. *ASYMP10* is derived from census sites taken in subsets of 1–10; the 95% confidence interval of this asymptote is represented in Figure 3. If a selection of only 10 sites per region were censused, all of the six pairwise comparisons would show significantly different regional species counts except for CA and WA. Thus, standardizing for census number does not remove inequitability in species richness S_T among regions, a conclusion supported by differences in jackknife estimates S_J and a high correlation between S_T and S_J ($r = 0.997$) and between these measures and *ASYMP10*.

Other factors potentially influencing S_T include range of latitude, mean latitude, and total geographical area covered by the censuses
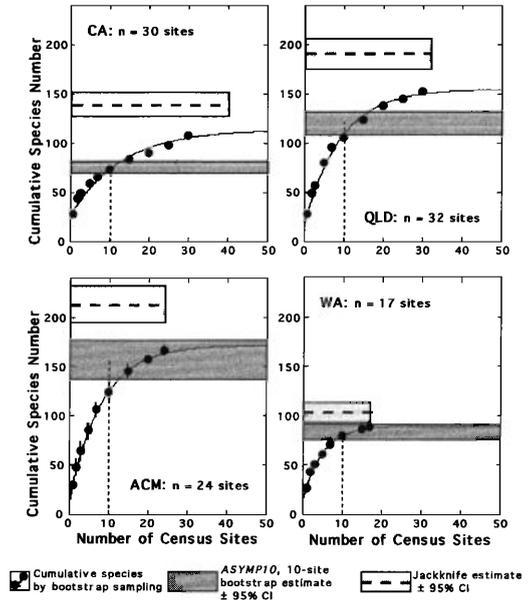

FIG. 3. Cumulative species number (ordinate) plotted as a function of number of sites censused (abscissa). Data points show cumulative species counts from simulations drawing increasingly large samples (numbers of sites) from field data. The fitted curve to these points is shown, with SD values around points in lower left (ACM sites). Regional species richness is compared using (A) jackknife estimates (dashed lines) with 95% confidence interval (lightly stippled) and (B) the asymptote (*Asympt10*) from a random drawing of 10 census sites (95% CI shown by densely stippled bar). Regional species totals are significantly different among regions.

within a region. Although those are not significantly correlated with S_T, S_J, or *ASYMP10* ($r = 0.35$ or less), the conspicuously lower S_T of the WA region does correspond to its reduced latitudinal range and the smaller geographical area encompassed by the woodlands there. All three measures of regional diversity (S_T, S_J, and *ASYMP10*) correlate with variance in vegetation structure VarHT (r varies between 0.56 [S_T] and 0.71 [*ASYMP10*]), and more strongly with the areas of the ellipses (Fig. 2) that measure regional variation in vegetation structure: $r = 0.62$ [S_T], 0.65 [S_J], and 0.88 [*ASYMP10*], but with df = 2, only r values >0.95 are significant. However, those results suggest that the wider the regional range of vegetation structure the greater the total number of bird species within the regional data set. The pattern is consistent with species turnover or replacement associat-
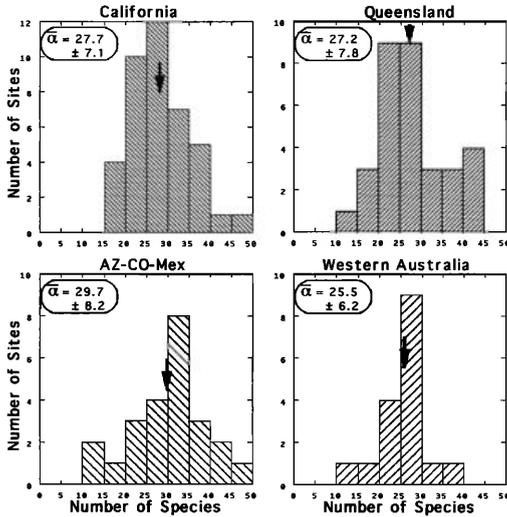
FIG. 4. Frequency distributions of α-diversity (within-site species totals) in four regions. Mean values do not differ significantly among regions, and likewise the ranges are also similar.

ed with differences in site separation and vegetation structure (i.e. with β- and γ-diversity components; see below).

Vegetation structure and bird species numbers.— Despite differences in vegetation structure, mean α-diversity is remarkably constant among regions (Table 1). Mean values range between 25.5 and 29.7 breeding species per site, and none of the differences are significant (ANOVA, Bonferroni correction, $P > 0.05$). Similarities among the regional α-diversities are in striking contrast to regional differences in S_T.

There is extensive variation in α-diversity (>4-fold) among sites (Fig. 4), both within and among regions. Two factors possibly influencing that variability are variation in vegetation structure and in latitudinal position. Profile area (AR) measures the total vegetation density at a site, and $\log(AR)$ consistently explains the highest proportion of variance in α-diversity (Figs. 5 and 6, upper). In North American oak sites (Fig. 5), $\log(AR)$ accounts for 26–28% of the variation in α-diversity; in the two Austra-
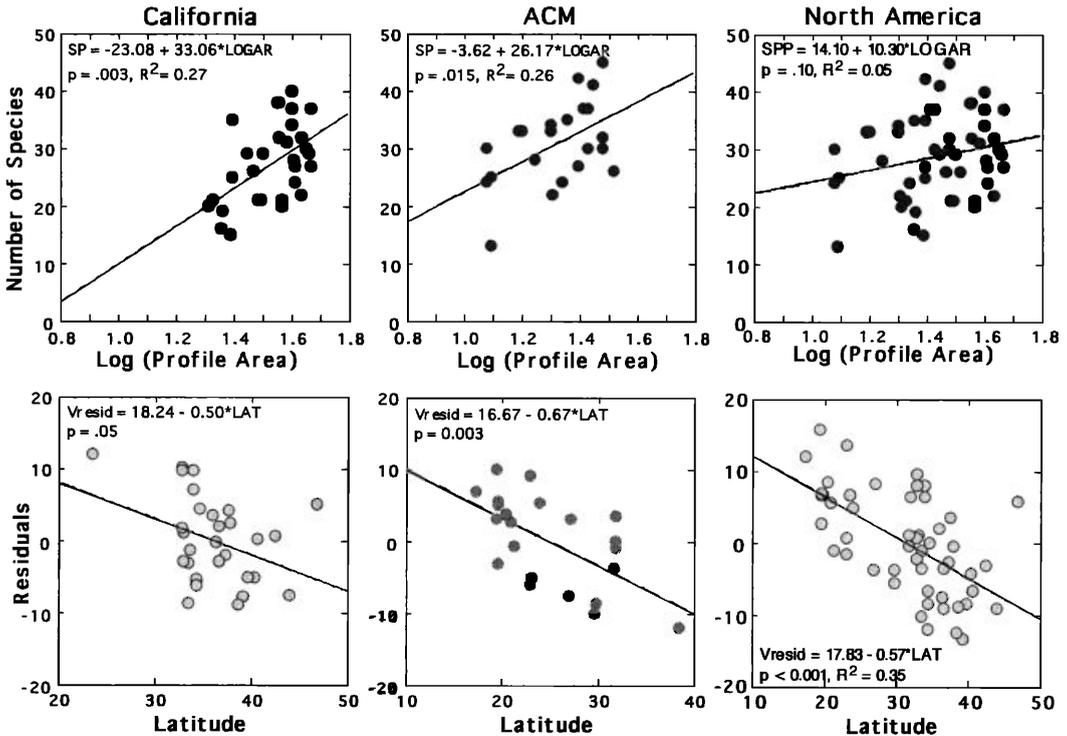

FIG. 5. Bird α-diversity of oak woodlands increases with log (Profile Area), a measure of overall vegetation density, with 26–27% of its variation accounted for (upper, left, and center). Residuals from these plots show significant latitudinal gradients in α-diversity in North America (lower, left and center). The two regions are combined to the right of the figure, with no differences to conclusions.
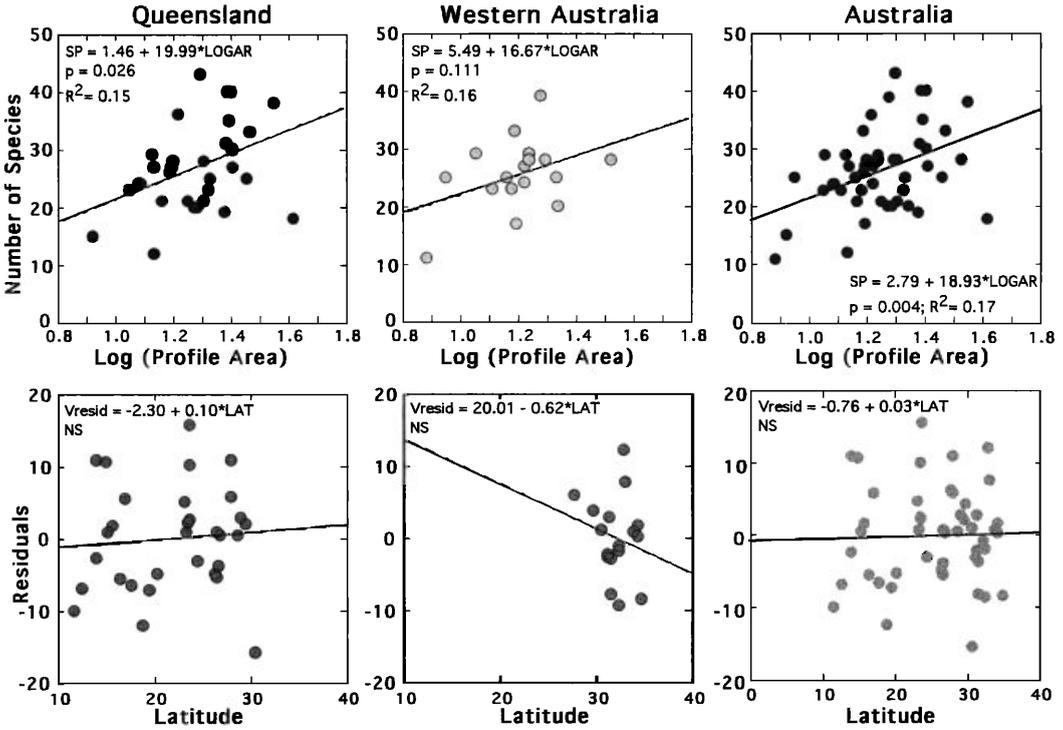
FIG. 6. Bird α-diversity of eucalyptus woodlands increases with log (Profile Area) in the two Australian regions, at similar rates (n.b. WA data, $n = 17$, NS; cf. QLD data, $n = 32$, $P = 0.026$), with 15–16% of its variation accounted for. Residuals from the (upper, left, and center) plots are plotted below (lower, left, and center), showing no latitudinal gradients in α-diversity exist. Combined plots (right) show same trends.

lian regions (Fig. 6), R^2 values are lower (15–16%; NS for WA region).

With α-diversity (*SPP*) as the dependent variable in multiple regression analysis, both *LAT* and log(*AR*) are incorporated as significant independent variables in ACM sites, only log(*AR*) in CA and QLD sites, and neither is significant in WA regressions. Residuals from *SPP*-log(*AR*) simple regressions are plotted against latitude to evaluate latitudinal effects on α-diversity while controlling for variation in vegetation structure (Figs. 5 and 6, lower; n.b. there are no significant relations between *AR* and *LAT* within regions). Significant effects of increased α-diversity with decreasing latitude occur in both North American (CA, ACM), but neither of the Australian (QLD, WA) regions. Because of the variable latitudinal position and range of sites within regions, North American and Australian data, respectively were treated in combined analyses. Although that combination lowered the predictive power of log(*AR*) with respect to species number in the North

American data, conclusions for both continents are unaltered in the combined data sets (Figs. 5 and 6). With similar sample sizes and latitudinal range, there is a clear latitudinal trend of α-diversity in the North American, but not the Australian woodlands.

Vegetation structure and breeding bird density.— Breeding bird density (*DENS*) varies widely among sites, and was generally higher in CA and lower in WA sites (mean values in Table 1). Among regional contrasts, CA is significantly higher in breeding bird density than either QLD or WA (ANOVA, Bonferroni correction, $P < 0.05$). As with α-diversity, total bird density is related most closely to total vegetation density log(*AR*). In three of four regions (CA, ACM, QLD), total breeding bird density increases significantly with profile area (Fig. 7), and the slopes of those three regressions do not differ significantly ($P > 0.05$, with SE in the range 5.5–7.5). However, the percentage of variance in bird density attributable to vegetation density is small (14–23%). In WA, by contrast,
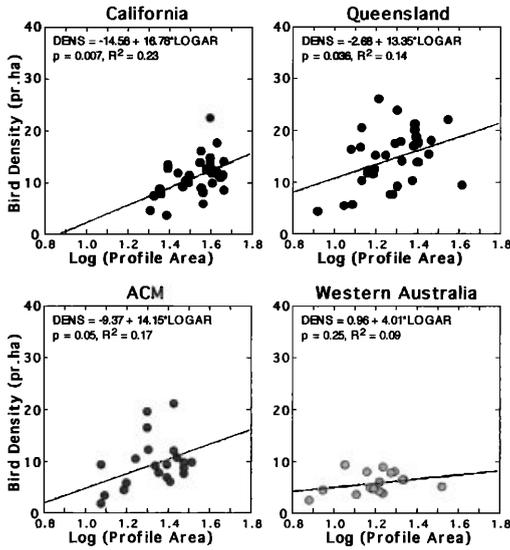
FIG. 7.   Variation within regions of total bird density (pairs per hectare) at census sites corresponds most closely with overall vegetation density, measured as log (Profile Area) at all census sites. The relation is not significant for sites in the WA region.
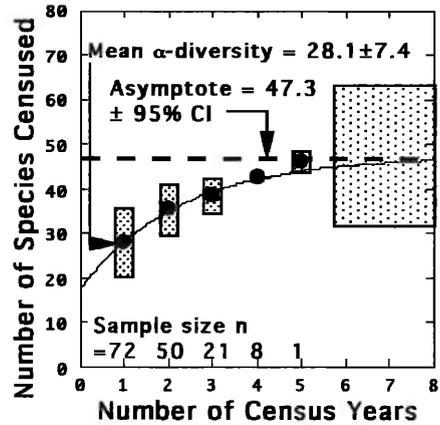

FIG. 8.   Census replicability between years is assessed for the larger data base from the CA region. The cumulative number of species censused at a site (ordinate) increases with the number of years the site is censused (abscissa; maximum 5 years). Mean cumulative species numbers and standard deviations are shown, with the fitted curve producing an asymptote (dashed line) with 95% CI (stippled area). Five years of census replication adds up to 19 extra species to average site α-diversity (28.1 species).

bird densities are narrowly constrained despite wide variation in vegetation structure.

Species turnover within and among sites, within regions.—Regional species totals (S_T) exceed mean α-diversity to the extent that there are different species represented at different census sites, that is, there is a turnover or replacement of species among sites within regions. Such turnover may be noise attributable to chance, sampling error, or environmental variations at census sites, or to systematic species turnover generated by differences among census sites in vegetation structure (β-diversity component) or geographical position (γ-diversity component).

To evaluate census variability within sites, I measure bird species turnover within sites, among years. Among censuses replicated within sites over time (among years), species differences may have several alternative explanations, including (1) sampling effects, wherein locally rare species are missed in any given year despite constant (low) density; (2) off-site effects, for example, species vary among years in density due to variation in over-winter survival; or (3) interyear site variations that influence site attractiveness to certain species in a given year. Such interyear differences, here

called "replication noise," combine sampling effects and environmental noise that are measurable in combination but not separable in practice. For CA sites, replication noise is assessed in each of 40 sites censused in one to five separate years (not necessarily in adjacent years). Cumulative species recorded at a single site is an increasing function of number of years censused (Fig. 8), with an asymptote (fitted by least-squares nonlinear regression) estimated at ~19 species greater than mean α-diversity.

Temporal variation within sites together with numerical and spatial variation in bird populations will contribute jointly to this figure; this variation may be of an episodic nature or represent longer-term trends. Census similarity among years at a given site is a function of the interval between the censuses. Species turnover between censuses in adjacent years averaged 16.3%, and increased asymptotically to 26.6% after intervals of five or more years (Fig. 9). Thus, once-replicated censuses would add between 4.6 and 7.5 species, depending on the intercensus interval. An alternative estimate of replication noise is given by the intercept of regressions of *VGTURN* and *DIST* on the *SPTURN* axis as described below.
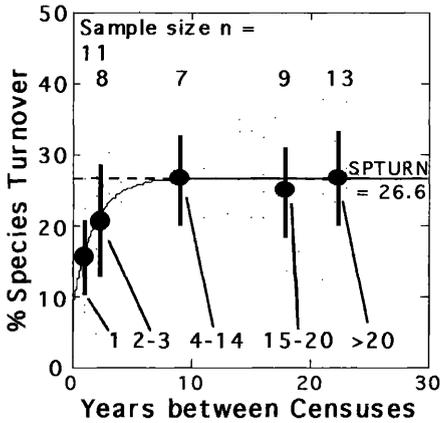
FIG. 9. Similarity between replicated censuses at a single site decreases with increasing time interval between the censuses, but only up to intervals of 8 to 10 years. Species turnover between replicated censuses increases to a fitted asymptote of 26.6%, indicating that one census replication adds 4.6–7.5 species (depending on time interval between replicates, 1 to 20 years).

Species turnover with differences in vegetation structure (β-diversity) and inter-site distance (γ-diversity).—One possible systematic effect on species turnover is via differences between sites in vegetation structure, a measure of β-diversity. Regions with similar α-diversity but different S_T may differ in a β-diversity component, such that species are replaced more

rapidly per change in habitat (vegetation) in regions with higher S_T.

Secondly, species turnover may be a function of the relative isolation (and its correlates) of two sites, with differences in species lists attributable to faunal differences, histories, or barriers to dispersal related to discontinuities in habitat distribution. Although such differences among sites have potentially complex explanations, they can be quantified by species turnover relative to the most obvious correlate of relative isolation, intersite distance. Species turnover with inter-site distance is the simplest measure of γ-diversity. Regional diversity S_T is thus a combination of several diversity components.

To examine systematically β- and γ-diversity components, species turnover *SPTURN* was cast as the dependent variable in multiple Mantel regressions with *VGTURN* and *DIST* as independent variables. As *SPTURN* increases rapidly with increasing *DIST* at low values and only slowly at higher values, *DIST* was log-transformed. The variables are subscripted as T (*SPTURN*), V (*VGTURN*), and D (*DIST*) in coefficients below and in Table 2, where simple and partial correlation coefficients and regression coefficients for those analyses are given. Species turnover increases significantly with increasing *VGTURN* in CA and QLD site comparisons. In WA sites, simple Mantel correlation r_{VT} is significant ($P < 0.01$), but the partial

TABLE 2. Simple[a] and partial[b] Mantel correlation coefficients, and simple[c] and partial[d] Mantel regression coefficients in analyses of species turnover (*SPTURN*) as dependent variable, difference in vegetation structure (*VGTURN*) and intersite distance (*DIST*) as independent variables (see Fig. 10). Subscripts are represented as T, V, and D respectively.

Region		r_{VD}	r_{VT}	r_{DT}	$r_{VT,D}$	$r_{DT,V}$	b_{VT}	b_{DT}	a	R^2	$b_{VT,D}$	$b_{DT,V}$
					Full range of *DIST*						$DIST < 500$ km	
CA		0.035	0.144	0.347	0.141	0.346	12.46	10.96	49.37	0.140	6.65	26.71
	P		0.02	<0.01	0.03	<0.01						
	n				435						221	
ACM		0.044	0.260	0.430	0.267	0.434	18.47	11.19	64.95	0.243	6.12	57.94
	P		0.07	<0.01	0.07	<0.01						
	n				231						95	
QLD		0.055	0.264	0.575	0.284	0.582	26.68	22.94	67.09	0.385	29.06	45.48
	P		<0.01	<0.01	<0.01	<0.01						
	n				496						170	
WA		0.309	0.362	0.425	0.268	0.353	26.69	13.93	59.85	0.239	18.05	50.71
	P		<0.01	<0.01	0.07	0.06						
	n				136						106	

[a] Columns 1–3.
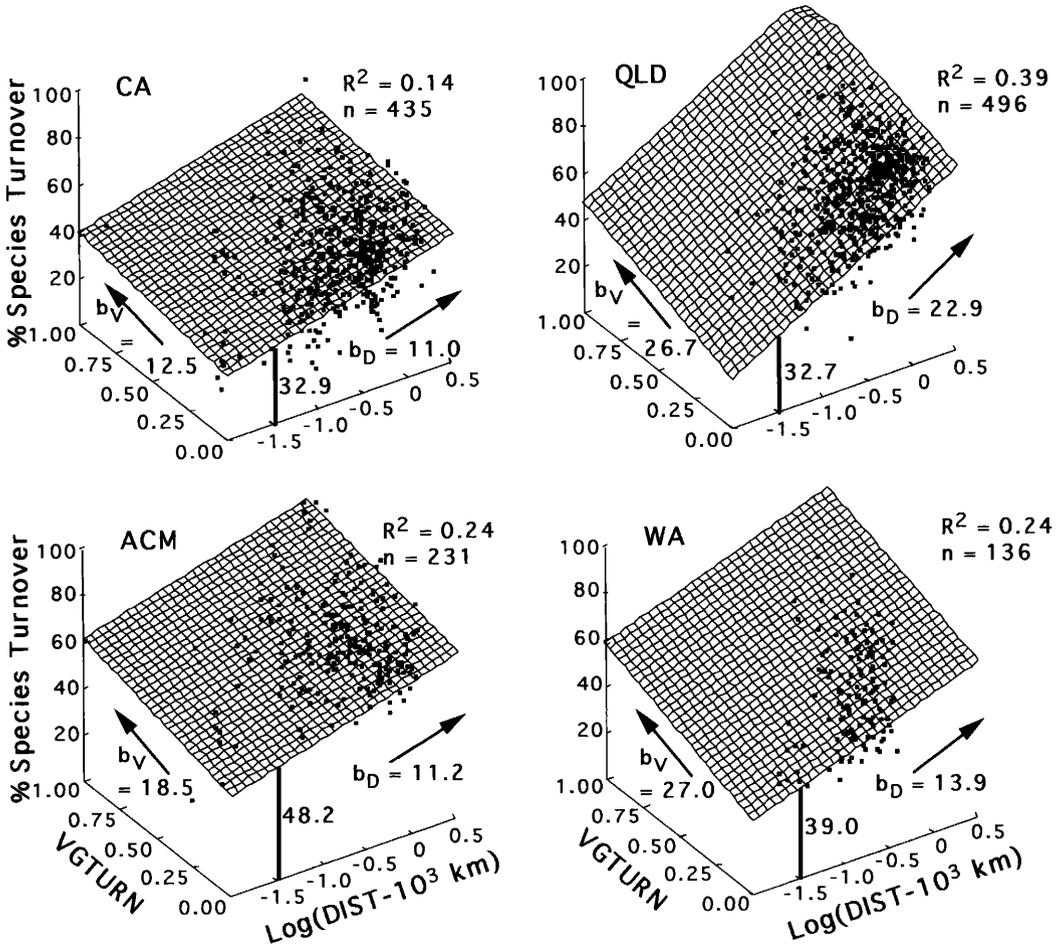[b] Columns 4–5.
[c] Columns 6–7.
[d] Columns 10–11.

FIG. 10. Species turnover is assessed by comparing census sites within regions, each pair of sites sharing some species in common and each site having unique species. Species turnover (*SPTURN*, ordinate) is related to both difference in vegetation structure between sites (*VGTURN*) and distance apart of sites (*DIST*); turnover with respect to those two independent variables measures β- and γ-diversity, respectively. Simple Mantel regression coefficients are included in the figure (*b*-values); *DIST* effects are all significant, *VGTURN* is a significant effect in all regions except ACM. The fitted multiple linear regression is shown by the fitted surface. The intercept of the regression plane on the vertical (species turnover) axis is a measure of "replication noise," and is evaluated in the figures at *VGTURN* = 0, *DIST* = −1.5. Replication of censuses at adjacent sites with similar structure produces a species turnover between 33–48%.

correlation coefficient $r_{VT.D}$ is weak, as it is also in ACM sites (P = 0.07). Simple and partial Mantel correlation coefficients r_{DT} and $r_{DT.V}$ between *SPTURN* and *DIST* are significant in all four regions (P < 0.01), except that the partial correlation is weak in WA (P = 0.06).

The Mantel regressions are shown in the three-dimensional plane in Figure 10; the coefficients b_{VT}, and b_{DT}, the constant values a, and coefficients of determination R^2 are given in Table 2. From the equations, I evaluate *SPTURN*

at *VGTURN* = 0 and *DIST* = −1.5 (an arbitrarily small value of site separation) to give estimates of replication noise. Those evaluations vary between 33 and 48%, and are included in Figure 10. The coefficients of determination are low to moderate (14%, CA; to 39%, QLD), indicating that a majority of the variation in species turnover remains unexplained.

Because species turnover generally slows with increasing values of *DIST*, I evaluated partial Mantel regression coefficients for sites sep-
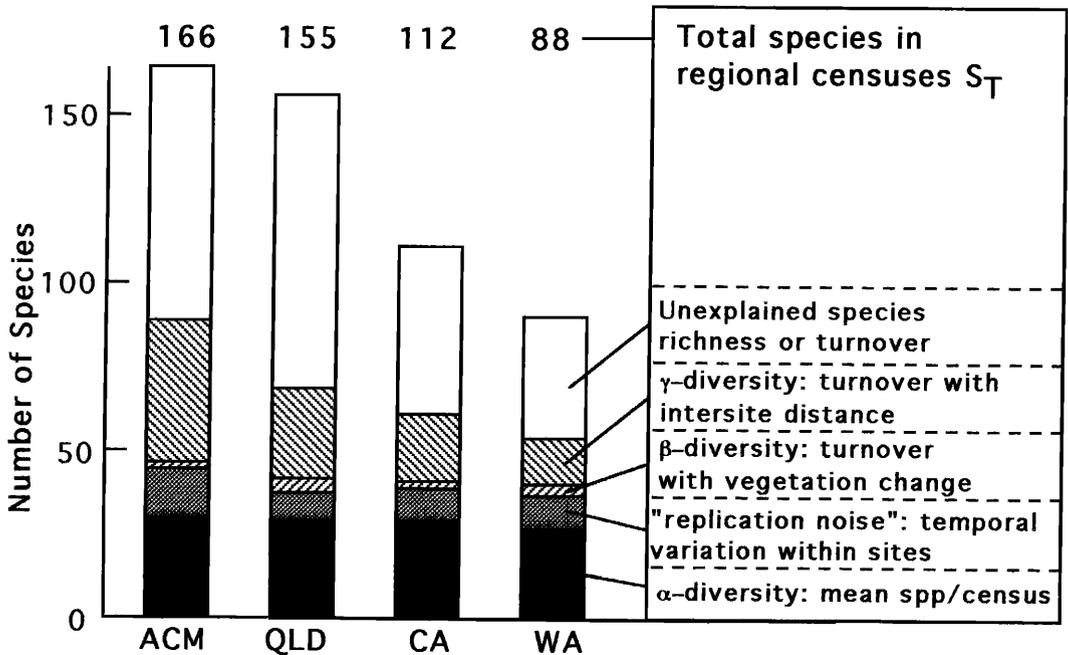
FIG. 11. Regional bird species totals S_T are show at the top of figure, and below are represented the species "accounted for" by within-site α-diversity and its replication noise, and species turnover between sites (β- and γ-diversity). The remaining 41% (WA) to 56% (QLD) of S_T is termed "unexplained turnover." S_T is strongly correlated with γ-diversity, but clearly factors other than inter-site distance promote species turnover between sites. Quantification of historical effects and efficacy of barriers to dispersal (e.g. topography, fragmentation, intervening habitat, etc.) is suggested for further research.

arated by $DIST \leq 500$ km. A comparison of the coefficients for the full and restricted data sets shows that the restriction to comparisons among closer sites reveals higher turnover rates with $DIST$ in all regions, and with $VGTURN$ lower turnover rates in North American sites and somewhat higher rates in the Australian sites (Table 2, last two columns).

The number of species contributed to the regional totals by β- and γ-diversity components is estimated first by extrapolation of species turnover rates with respect to site separation distances and differences in vegetation structure, given the observed ranges of $DIST$ and $VGTURN$ within each region. Second, the number of species contributed by given values of species turnover is computed. For example, from the CA regression $a = 49.37$ turnover, $b_{VT,D} = 6.65$ and $b_{DT,V} = 26.71$. As $VGTURN$ and $DIST$ have ranges of 0.9 and 2,666 in the CA data set, overall species turnover associated with vegetation change and site separation is calculated as 6.0 and 71.2%. With CA α-diversity = 27.7,

the latter figure, for example, adds 27.7–c, or 19.7 species, where $71.2 = 100(1 - c/27.7)$.

Summary figures that break down regional species totals into the components discussed here are shown in Figure 11. Overall, α-diversity is nearly constant among regions. Replication noise is highest in ACM (14.3 species), the region with the highest species richness. The β-diversity components are relatively small, as expected within a single habitat (woodlands) with only modest variations in vegetation structure among sites; β-diversity adds 1.6 species to each North American region, 3.2–5.5 species to WA and QLD regional totals. In contrast, variation in γ-diversity is conspicuous, and highest in regions with high regional species totals. It correlates strongly with variation in S_T, $r = 0.92$, and in S_J, $r = 0.85$. Figure 11 shows that a large component of regional species richness remains unaccounted for, especially in the regions of highest S_T (ACM, QLD); potential explanations are discussed below.

DISCUSSION

The comparative approach adopted here reveals that site α-diversities in these woodlands show similar average values in four regions on two continents (Table 1). Further, variations in site α-diversity (Fig. 4) respond to variation in vegetation structure in similar ways among regions (Figs. 5 and 6). Census replicability is estimated directly at CA sites, at which a single replication might yield five to eight new species, depending on inter-census interval, and frequently repeated censuses at a site might add as many as 19 species to the site's cumulative total. Replication is assessed indirectly from the regressions in Figure 10, where the $(0, -1.5)$ intercept identifies nearby sites with the same vegetation structure. Such assessments add 9 (CA, QLD), 10 (WA), or 14 (ACM) species to a one-site census, and generally accord with the direct measurements at CA sites.

Given the relative structural similarity of the woodlands, β-diversity is expected a priori to be low. In contrast, species turnover relative to intersite separation distance, γ-diversity, is both high and highly variable among regions, and shows the greatest potential to account for regional differences in species totals S_T (Figs. 11 and 12). In ACM, for example, a DIST partial coefficient of 57.9 and an inter-site range of 2,351 km indicate a γ-diversity contribution of 40.5 species, and a complete turnover of species over 1,727 km.

With unexplained turnover conspicuous in Figure 11, clearly a complete accounting for regional differences in S_T is as yet lacking. Several factors may explain the remaining or residual turnover, but those are more difficult to assess quantitatively. Two such factors, historical effects and topography, are discussed below.

Historical effects may account in part for unexplained variation in turnover, as different regions have experienced different geological, climatic, and biotic histories, colonization events and their timing. Regions also differ in relative isolation, in the areal representation of the habitat under discussion, in barriers to dispersal (both past and present), and in areas of and accessibilities to different adjacent habitat types. Collectively those factors influence such basic evolutionary processes as speciation and extinction, and their understanding and evaluation is likely not possible from present-day census results.

Topographical factors other than distance provide barriers that enhance species turnover among sites. For example, changes in topography across a landscape are often associated with elevational, climatic, biotic (e.g. predators, competitors) changes. The use of intersite separation distance as a surrogate for that complexity of factors is clearly inadequate. Residuals from regression analysis of the North American data (Fig. 10), for example, correlate significantly to elevation differences between sites, accounting for an additional 11% of variation in SPTURN. In Australia, elevational differences among sites are slight, but habitat barriers (e.g. nonwoodlands) and their efficacy over evolutionary time scales would presumably be of primary importance.

Other results and information support the relevance of additional factors, such as the areal extent of a habitat and distance from its epicenter, in influencing α-diversity and generating species turnover. Habitat area within regions or subregions may provide mass effects (Shmida and Ellner 1984, Cody 1993), such that areas with higher areal representation of the habitat support higher diversities. The areal extent of oak woodlands is higher on the southern ends of latitudinal gradients in CA and ACM, where latitudinal gradients in α-diversity are more prominent. A similar effect is observed in the oak woodlands of eastern North America, which are richest in species at intermediate latitudes (around 38–40°N) where their areal extent is larger (M. Cody unpubl. data; see also Rabenold 1979). Higher diversity toward the geographical center of distribution, and decreasing diversity both northward and southward, has been recorded in other habitats (Rabenold 1978, Blondel and Farré 1988, Lees et al. 1999). In Australia, eucalyptus woodlands are peripheral around the continent, between the arid interior and the wetter, coastal forests without latitudinal bias, and perhaps in consequence lack latitudinal gradients in α-diversity. However, within Western Australia a similar effect of habitat area was detected; census sites in eucalyptus woodlands further from their geographical epicenter produce lower values of α-diversity (Cody 1993). Regional differences in habitat availability may also contribute to diversity trends of upland bird species within Britain (Stillman and Brown 1998).

Questions involving the determination of regional diversity and its components are widely recognized as important; the patterns they illuminate are essential information sources for the conservation and management of natural resources. To date, ecologists have barely begun to frame those questions precisely and assemble data to address them adequately. The resolution of areal effects on diversity components, and investigation of the wide range of other topographical and historical influences on species turnover among sites, constitute one of the most interesting challenges to community ecologists.

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