On Large-Scale Dynamics and Community Structure in Forest Birds: Lessons from Some Eucalypt Forests of Southeastern Australia

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On large-scale dynamics and community structure in forest birds: lessons from some eucalypt forests of southeastern Australia

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SUMMARY

Models of ecological communities, including coevolved patterns of resource use among sympatric species (for example, 'resource partitioning'), are poor or inadequate representations of natural systems despite intense theoretical effort for many years. Some of these difficulties are due to a failure to recognize the necessary conditions for community patterns to develop, which are largely controlled by the dynamic characteristics of individual species. In continental bird communities – examples of which are considered here – these necessary conditions often will not be met owing to the mobility of most species. Here I document the degrees to which the large-scale dynamics (over hundreds of km) of individual bird species are expressed in community terms in five forest-habitat types throughout the year. These data demonstrate that continental bird communities are so dynamic that the conditions for the development of definite structure are unlikely to be met in either proximate or evolutionary time. The failure of community theories to account for and predict structure probably reflects too much concentration on mechanisms at inappropriate spatial scales.

1 INTRODUCTION

In the broadest sense, ecological communities consist of all living organisms (plants, animals, fungi, micro-organisms i.e. the 'food web') and the physical environment in which they live (Whittaker 1975). Community ecology is devoted to understanding the nature of interactions between organisms of different species. Interspecific interactions include mutualism, competition for resources or space, predation, parasitism and so on (Thompson 1988). There is both a contemporary aspect to the study of community ecology (how current communities 'work') as well as an evolutionary perspective, so that much of the interpretation of patterns seen in communities has been interpreted in evolutionary terms (see Roughgarden 1979).

Although communities are potentially all-encompassing – inclusive of all living components – there has been a strong tendency for workers to concentrate on certain components of communities (e.g. MacArthur 1971) so one often reads of bird communities, zooplankton communities etc. I use this limited sense of the term community in the remainder of this paper. This restricted usage isolates one part of the web and concentrates on the relations among these species and the resources they use. Much work (especially theory) involves modelling these more limited ecological communities as coevolved systems in which certain structures might be expected to persist for long periods and so should characterize contemporary communities (Mac Nally 1995*a*: pp. 216–224). The differentiation of resource use among similar, potentially competing species ('niche partitioning'; see Schoener 1974) is a topic that has relied heavily on the coevolutionary approach.

Unfortunately, a coherent understanding of communities continues to elude ecologists at least partly because of inadequate recognition of the relationship between community 'dynamics' and community 'function'. Dynamics are the rates of change of the spatial and temporal characteristics of communities and especially of constituent populations. They also involve the rates of interchange of individuals of the same species among populations occupying different areas or habitats by dispersal and migration (see Pulliam 1988; Pulliam & Danielson 1991).

On the other hand, ecological function is the 'rôle' of a population within a community and, in many respects, represents the characteristics of most interest to a deterministic, causal understanding of the way in which communities work. Rôles can be viewed at two levels. The first is the classical trophic positions of populations within food webs in which populations are regarded as decomposers, detritivores, producers, primary consumers and so on (see Polis 1994). This picture is closely related to the passage of energy and nutrients through food webs. The second level focuses on both the resources used and the ways in which they are used, namely, the 'guild' approach (see Terborgh & Robinson 1986; Hawkins & MacMahon 1989; Simberloff & Dayan 1991 for reviews). Guilds are sets

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of species that routinely use the same resources (for example, seeds or nectar as food, or tree-hollows for breeding/shelter) and gather or utilize those resources in similar ways (Root 1967). The explosive increase in the popularity of the guild concept (see figure 1 in Hawkins & MacMahon 1989) probably indicates that the classical trophic-level picture says little about the mechanisms contributing to within-trophic level diversity, much of which is due to radiation in the use of microhabitats and feeding techniques (Mac Nally 1994*b*).

How do dynamics affect interpretations of community function? First, if the local community consists of populations of species that vary greatly in abundance over relatively short timescales (compared with generation times) due to dispersal and migration, then it becomes difficult to interpret 'local structure' within the community as due to local processes (e.g. competition between species) alone. That is, the conventional Lotka-Volterra models of interacting competitors, which involve essentially isolated competing populations (see Roughgarden 1979: 411 ff.), are probably invalid. Second, the ecological features of a species are unlikely to be fashioned at the local scale of the population and probably reflect a more widespread adaptive response to the habitats and biotas to which the species as a whole is exposed (see Bock 1987). Thus the degree of dynamism evident in the populations of a community and the vagility of species each have a large bearing on how one views the reasons for the observed structure of a community. This means that certain conditions must be met for community structure and especially differentiation of resource use among competitors to be interpretable as the outcome of interspecific interactions at the local scale. What are these conditions?

Following Schluter & McPhail (1992), Taper & Case (1992) listed the six necessary conditions for the unambiguous demonstration of the morphological divergence of species pairs due to interspecific competition. These were: (i) differences between sympatric populations must exceed differences between allopatric populations; (ii) these statistically significant differences must have a genetic basis; (iii) differences cannot be due to the sources of colonists; (iv) morphological differences correspond directly to differences in resource use; (v) there is competition for the resources recognized in step (iv), and competitive intensity must increase as similarity increases (and vice versa); and (vi) morphological differences between sympatric and allopatric populations cannot be due to shifts in the structure of the resource base.

More generally, ecological differentiation need not be expressed purely in morphological terms but behaviour and other aspects may also be important. In addition, it is rare for species pairs to operate in an 'ecological vacuum,' so that the community context is more appropriate. Thus I would replace the six conditions of Taper & Case (1992) by the following eight necessary conditions under which coevolutionary ecological differentiation among the local contingent of (animal) species might be expected to occur.

1. The same set of consumer populations must occur together for periods of time that are long in relation to the typical generation lengths of the consumer species (the 'co-occurrence' condition).
2. The availability of resources upon which the consumers depend must be relatively constant for long periods of time relative to the typical generation lengths of the consumer species ('resource constancy').
3. Resources must be in chronically short supply ('resource limitation').
4. Climatic shifts (and associated vegetation changes) must not lead to monotonic changes in the relative differences in environmental suitability among populations ('environmental impartiality').
5. Recruitment must be deterministically and highly correlated with resource acquisition (i.e. recruitment must reflect the success with which individuals within the populations acquire resources: 'reflective recruitment').
6. Recruitment must be almost entirely internal (i.e. recruits are generated locally so that there is the potential for morphological, behavioural or physiological differentiation that is relatable to local processes: 'local recruitment').
7. Populations cannot be subject to the influx of conspecific individuals from other populations ('closure').
8. Exploitation competition must be the dominant interaction among species within the community, operating at intensities sufficient to offset intraspecific competition (including territoriality, cannibalism, etc.) and the impact of predators and parasites ('saturated environments').

These conditions broadly relate to the occurrence of a recognizable, integrated 'community' (the co-occurrence condition), resource limitation (resource constancy and limitation), environmental consistency (impartiality), local recruitment (reflective and local recruitment), lack of 'contamination' from other sources (closure) and the predominance of one ecological process (saturated environments).

This paper is the culmination of my analyses of the community dynamics of forest and woodland birds in central Victoria, Australia. My intention is to describe the dynamism of forest and woodland bird communities over a relatively extensive spatial domain (ca. 1.8×10^4 km^2). Dynamism is expressed in several ways but especially in relation to the dynamic strategies and habitat specificity of different species. Knowledge of the relative proportions of sedentary and vagile species and of habitat specialists and generalists dictates the degree to which an interpretation of community structure based on local interspecific interactions is warranted. To address these issues, I integrate the components of community structure and dynamics introduced in previous publications (see, for example, Mac Nally 1989, 1990*a*,*b*,*c*, 1995*b*).

2. METHODS

(*a*) *Study region and plots*

The large-scale nature of the study was achieved by selecting study sites from along a survey line that spanned 250 km in central Victoria, Australia. This survey line was oriented north-south so that it crossed the Great Dividing Range (GDR), which runs east-west in central Victoria (see figure 1, Mac Nally 1995*b*). The most northerly plot was at Undera in the Goulburn River valley (36°28′ S, 145°13′ E), whereas the most southerly plot was at Nepean, not far from Cape Schanck (38°28′ S, 144°52′ E). The north-south orientation allowed five of the main forest and woodland habitats of central Victoria to be surveyed (see DCFL 1984). The selection of habitats included: (i) open woodlands of the Goulburn River valley, consisting mainly of River Red Gum (*Eucalyptus camaldulensis*) and Grey Box (*E. microcarpa*); (ii) woodlands dominated by Red Ironbark (*Eucalyptus tricarpa*) and Grey Box on the stony rises of central Victoria; (iii) an assortment of forests and woodlands in the northern and southern foothills of the GDR consisting of a variety of box, peppermint and stringybark species (all *Eucalyptus*); (iv) tall montane forests of the GDR, mainly of Mountain Grey Gum (*E. cypellocarpa*), Candlebark (*E. rubida*), Messmate Stringybark (*E. obliqua*), Blackwood (*Acacia melanoxylon*) and Mountain Ash (*E. regnans*); and (v) woods of the southern lowlands and maritime plains, mostly of Gippsland Manna Gum (*E. pryoriana*), Swamp Gum (*E. ovata*) and small amounts of Messmate. For brevity, these five main forest and woodland types are referred to by using the mnemonics: RGGB (Red Gum-Grey Box), RIGB (Red Ironbark-Grey Box), FHNS (foothill woodlands), MGCMA (montane forests) and GMG (Gippsland Manna Gum). The structural characteristics of the five habitat types are described in detail elsewhere (Mac Nally 1989).

There were four 'replicate' plots of each of these types of habitat, making 20 plots in all. Replicates of each habitat type were separated by at least 10 km and as much as 140 km depending upon the geographic distribution of the habitat. The use of replicates provided information on the degree to which patterns displayed by bird species were consistent among plots of the same general physiognomy and floristics (see Mac Nally 1989). Study plots were areas of woodland or forest that subjectively appeared to be relatively homogeneous in structure and floristics and were set in more extensive tracts of similar forest or woodland.

(*b*) *Censuses*

Censuses of the avifaunas at each location were undertaken once during each season. The seasons were regarded as: (i) summer: December 22 1985 to March 21 1986; (ii) autumn: March 22 1986 to June 21 1986; (iii) winter: June 22 1986 to September 21 1986; and (iv) spring: September 22 1986 to December 21 1986. All individual birds were identified by sight and/or by voice. A detailed description of censusing methods appears in Mac Nally (1995*b*).

(*c*) *Dynamic 'strategies'*

The dynamics of individual species of birds were characterized with respect to the study region or, more precisely, the habitats of the survey line. This means that conclusions derived here are sample based ones referring to the 20 sites of the survey-line and cannot be extrapolated directly to larger spatial scales.

Table 1. *Definitions of spatial and temporal components of dynamic strategies*

(E eurytopy; O oligotopy; S stenotopy; R residency; I itinerancy; and M migratory.)

term	characteristic
spatial	
E	occupation of all habitats
O	occupation of more than one but not all habitats
S	occupation of just one habitat type
temporal	
R	no significant differences in mean density with respect to season, and no significant habitat by season interaction
I	no significant differences in mean density with respect to season, but significant habitat by season interaction
M	significant differences in density among seasons

Given this proviso, the strategy displayed by a species within a region consists of a spatial component and a temporal component (see table 1). The former relates to the breadth of habitat tolerance displayed by species with respect to the five main habitat types considered here. If a species occupies all habitats, then the species is eurytopic on the survey line (= eurytopic + ubiquitous classes of Mac Nally 1995*b*). If a species occurs in more than one but not in all habitats of the survey line (for example, RIGB and GMG, but not FHNS, MGCMA or RGGB), then the species is termed 'oligotopic'. Species restricted to a single habitat type (e.g. just RGGB, or only GMG) are called 'stenotopic'.

There are three temporal strategies but distinguishing between them requires information on the seasonal changes in density of a species in each habitat. If densities do not change significantly from season to season in each occupied habitat, then a species is regarded as a regional resident. If the mean seasonal densities do not differ significantly but there is a statistically significant interaction between the habitat and season effects, then the species is regarded as a regionally itinerant one. Individuals of itinerant species appear to move among habitats so that increases in some habitats occur concurrently with compensatory decreases in other habitats. There may or may not be a significant habitat effect because itinerant species may occupy only some of the habitats. In the third temporal strategy, densities differ significantly from season to season so that the species can be thought of as a regional migrant, in the usual sense.

Note that only the 60 species classified in table 6 of Mac Nally (1995*b*) are included in the following analyses of spatial and temporal strategies. The strategies of the remaining 29 species are too uncertain at this time to be considered, but these species are unlikely to have a major impact because most were either sporadically encountered or rare. Data consist of the summation of densities (over species) for each type of strategy in a given plot during each season.

(*d*) *Statistical analyses*

The survey was conducted so that changes in densities could be analysed as a balanced, repeated measures analysis of variance. This design can be represented by using the following linear model:

$$Y_{ijkl} = \mu_{....} + \eta_i + \pi_{j(i)} + \psi_k + \gamma_l + (\eta\psi)_{ik} + (\eta\gamma)_{il} + (\psi\gamma)_{kl} + (\eta\psi\gamma)_{ikl} + \epsilon_{(ijkl)}. \quad (1)$$

In equation 1, Y_{ijkl} is the measurement for strategy k in replicate j of habitat i in season l, $\mu_{....}$ is the overall mean, η_i is the mean value for habitat i, $\pi_{j(i)}$ is the specific effect of a given site (i.e. the object upon which repeated measures are performed), ψ_k is the average for strategy k, γ_l is the average for season l, bracketed terms denote interactions between main factors and $\epsilon_{(ijkl)}$ is the residual or unexplained variation. Note that $j(i)$ means that information for individual sites is nested within a particular habitat type.

I derived expected mean squares for the analysis of variance based on equation 1 by using the protocol outlined by Neter *et al.* (1990, pp. 1016–1021). Season and strategy were regarded as fixed factors. Habitat is a random factor because the set of habitats used here is only representative (rather than inclusive) of those encountered in the region.

In complex statistical designs involving hierarchical structure, some terms (particularly interactions of main factors) accumulate large degrees of freedom. This often yields statistically significant F-tests for these terms, but the significance may have little ecological meaning because of the inflated degrees of freedom. A solution to this dilemma is the use of variance components, which allow an assessment of the degree to which each term contributes to variation in the data. Thus the expected mean squares derived above were used to compute the variance components (for example, Vaughan & Corballis 1969; Dwyer 1974; Susskind & Howland 1980).

The 5% significance level is used throughout and is denoted by an asterisk (*). Residuals were assessed to determine whether transformations were necessary to conform with ANOVA assumptions, but none were needed. Where appropriate, *post hoc* comparisons of group means were conducted by using Ryan's procedure (Day & Quinn 1989).

3. RESULTS

(*a*) *Dynamics of total densities*

There were no significant differences among the five habitats in relation to the mean annual densities (averaged over the four seasons) (see figure 1). The annual means ranged from 79 (RIGB) to 96 (GMG) birds per 10 ha, but the magnitude of this difference was small given plot-within-habitat variation (see table 2). I could detect a variance ratio of 2 between the habitat and plot-within-habitat variances with probability 0.83 (see table 2), so among-habitat differences in density are unlikely to be ecologically significant. Total densities averaged over the entire region (i.e. irrespective of habitat) were not significantly different among seasons (see figure 2*a*, table 2). The total, mean regional density ranged from 84 (autumn) to 88 (winter) birds per 10 ha. Given the sampling design, a deviation of ±20 birds from the average of 86 in two of the seasons would be almost certainly detected, as would an even distribution of means between 76 and 96 birds per 10 ha (see table 2).

(*b*) *Regional dynamics of temporal and spatial strategies*

The absence of seasonal differences in total densities over the entire region is explicable when relative total densities of the three temporal strategies (resident, itinerant, migrant) are considered. The five habitats were numerically dominated by regionally resident species (see figure 2*a*). Averaged over both season and habitat, the total densities of resident, migrant and itinerant species were 63, 6 and 17 birds per 10 ha, respectively. Recall that the definition of residency is 'no significant differences in density [of a given species] between seasons', so that this dominance of resident species largely accounts for the absence of strong seasonal differences within the entire region. Note also that itinerant species such as the Golden Whistler (*Pachycephala pectoralis*) showed no significant differences between seasons, although they do wax and wane seasonally among habitats. Thus, together resident and itinerant species averaged about 93% of all individuals.

Spatial strategies were dominated by oligotopic species, with relatively small numbers of stenotopic species or 'habitat specialists' (see figure 2*b*). Averaged over habitat and season, the densities for oligotopic, eurytopic and stenotopic species were 48, 27 and 9 birds per 10 ha respectively (see figure 2*b*). Thus, species with either intermediate or catholic habitat tolerances (with respect to the five habitats used here) numerically dominated the central Victorian region, while only about 11% of individuals are habitat specialists.

(*c*) *Habitat-specific dynamics of temporal strategies*

Regional residents predominate as do species showing some flexibility in habitat use (see § 3*a*,*b*). I wish to build on these regional results by considering patterns evident in each habitat type separately.

The strength of the differences in temporal strategies (i.e. residents, migrants etc.) is shown by the 82% of variation being attributable to this factor. Neither the season nor habitat factors were significant, but several of the interactions were (see table 2). The significance of the habitat by strategy by season (three factor) interaction is largely due to different patterns displayed among habitats by itinerant species. Densities of itinerant species differed little seasonally in FHNS and RGGB habitats. However, there was a strong autumn-winter peak in RIGB but a spring-summer peak in GMG and MGCMA (see figure 3). Similarly, migrants maintained much the same densities through time in RGGB and RIGB but were virtually absent in the autumn and winter in GMG, FHNS and MGCMA (see figure 3). The statistically significant habitat by strategy interaction

Table 2. *Repeated measures* ANOVA *of densities of temporal strategies* (*repeated measures on strategy and season factors, model 1*)

(MS denotes mean square; * indicates significant at the 5 % probability level; n.s. denotes not significant at the 5 % probability level; VC indicates the variance component. There are: 5 habitats (random factor); 3 strategies (fixed factor: resident, migrant, itinerant); and 4 seasons (fixed factor).

factor	d.f.	MS	*F*-ratio	VC d.f. test	(%)
[a]habitat (η)	4	354.3	1.01 n.s.	4, 15	≅ °0
plot within habitat (π)	15	351.0	—	—	2
strategy (ψ)	2	72,247.0	138.32*	2, 8	82
[b]season (γ)	3	23.0	0.10 n.s.	3, 12	0
habitat, strategy ($\eta\psi$)	8	522.3	4.27*	8, 165	2
habitat, season ($\eta\gamma$)	12	221.2	1.81 n.s.	12, 165	1
strategy, season ($\psi\gamma$)	6	400.5	2.08 n.s.	6, 24	1
three factor ($\eta\psi\gamma$)	24	192.7	1.58*	24,165	2
residual (ϵ)	165	122.3	—	—	11

[a] Denotes power to detect $\sigma^2_\eta/\sigma^2_\pi = 2$ assuming $\sigma^2_\eta \geqslant \sigma^2_\epsilon$, with d.f. 4, 15 and $\alpha = 0.05$ is 0.83.

[b] Denotes power to detect seasonal mean distribution of 66, 86, 86, 106 birds per 10 ha (overall average is about 86) exceeds 0.95 (noncentrality parameter $\phi \cong 5.7$ with d.f. 3, 12 and $\alpha = 0.05$). Power to detect seasonal mean distribution of 76, 83, 90, 96 birds per 10 ha exceeds 0.95 (noncentrality parameter $\phi \cong 4.4$).

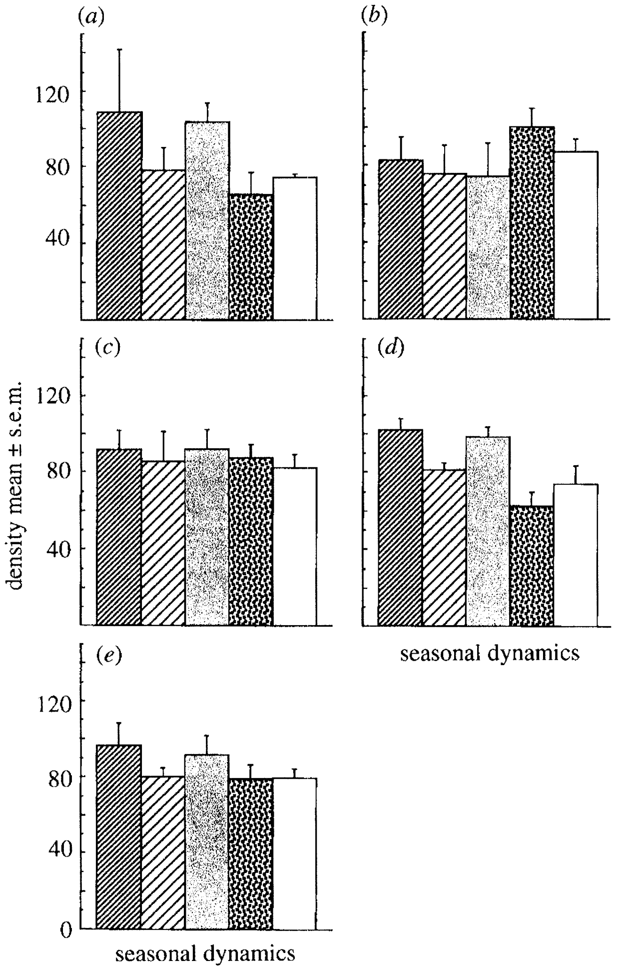

Figure 1. Seasonal dynamics: total densities of all species of birds during each season, and the seasonal average calculated over the annual cycle. Data are provided separately for each type of forest or woodland habitat, and are expressed as individuals per 10 ha: mean ± standard error (all $n = 4$). (*a*) summer; (*b*) autumn; (*c*) winter; (*d*) spring; (*e*) mean annual. (▩) GMG; (▨) FHNS; (▦) MGCMA; (▣) RIGB; (□) RGGB.

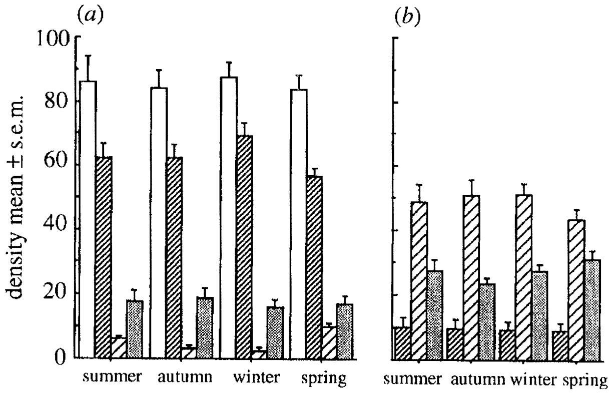

Figure 2. Total densities calculated over all 20 sites ('regional' averages). (*a*) Temporal strategies (□) all; (▩) resident; (▨) migrant; (▦) itinerant. (*b*) Spatial strategies (▩) stenotopic; (▨) oligotopic; (▦) eurytopic. Data are expressed as individuals per 10 ha: mean ± standard error (all $n = 20$)

(see table 2) reflects generally lower total densities of resident species in RIGB (and to a lesser extent RGGB) than in GMG, FHNS and MGCMA habitats, and the uniformly low densities of itinerant species in RGGB relative to the other habitats (see figure 3).

(*d*) *Habitat-specific dynamics of spatial strategies*

The regional dominance of oligotopic species (§ 3*b*) was evident in four of the five habitat types. In RGGB however, stenotopic species rivalled oligotopic ones, both averaged about 30 birds per 10 ha, whereas there were 19 individuals of eurytopic species (see figure 4). Stenotopic species comprised relatively few individuals in any of the other habitats; none were recorded for FHNS (see figure 4). Individuals of oligotopic species occurred in relatively consistent numbers in FHNS, MGCMA and RGGB habitats, but there were higher densities of oligotopic species in GMG during the spring-summer period and in RIGB in the autumn-winter period (see figure 4). Much of this variation is attributable to the migratory patterns of two species of

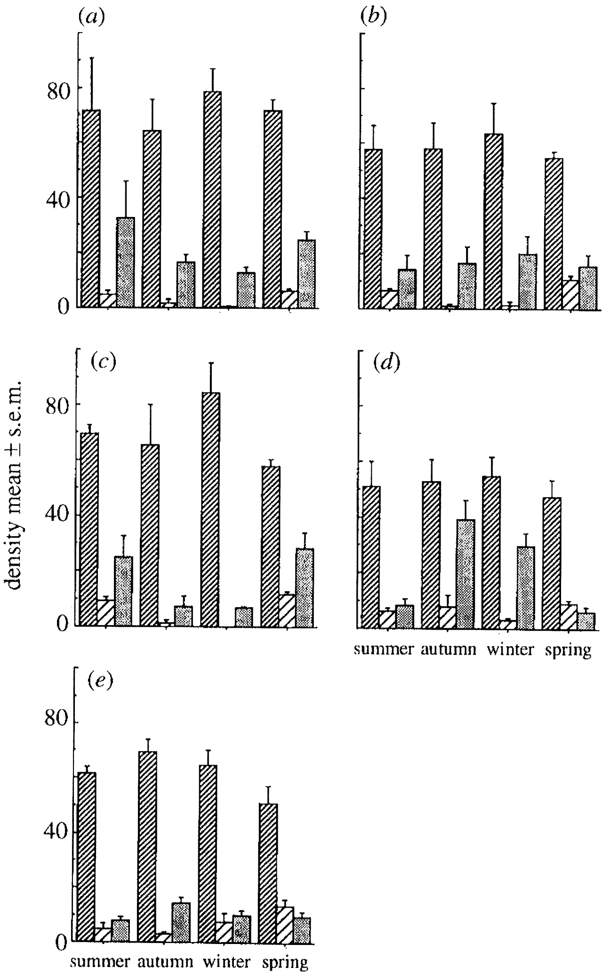

Figure 3. Seasonal fluctuations in each habitat of densities of each of the three temporal strategies. (*a*) GMG; (*b*) FHNS; (*c*) MGCMA; (*d*) RIGB; (*e*) RGGB. Data are expressed as individuals per 10 ha: mean ± standard error (all $n = 4$) (▩) resident; (▨) migrant; (▦) itinerant.

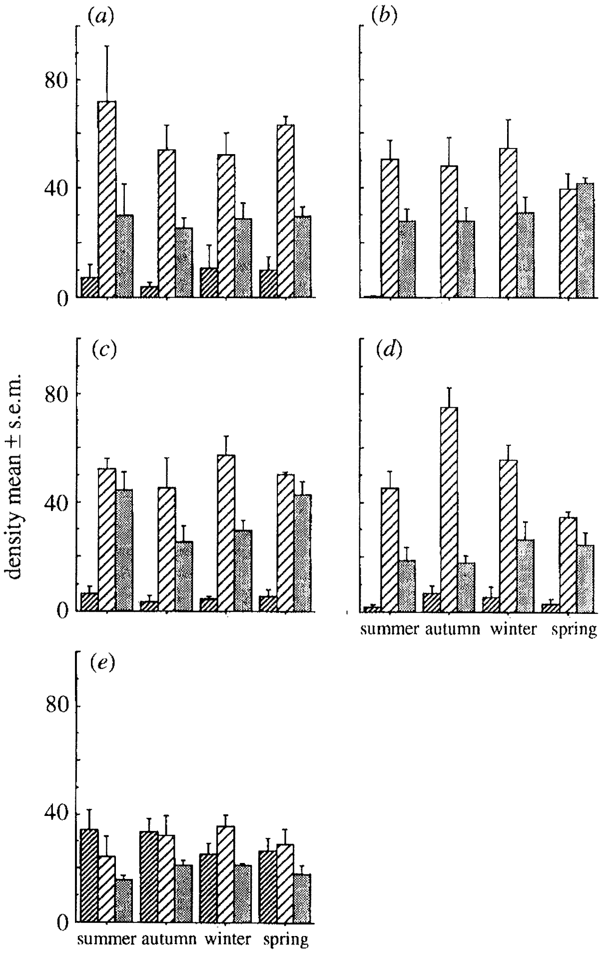

Figure 4. Seasonal fluctuations in each habitat of densities of each of the three spatial strategies. (*a*) GMG; (*b*) FHNS; (*c*) MGCMA; (*d*) RIGB; (*e*) RGGB. Data are expressed as individuals per 10 ha: mean ± standard error (all $n = 4$). (▩) stenotopic; (▨) oligotopic; (▦) eurytopic.

meliphagid honeyeater, the Red Wattlebird (*Anthochaera curunculata*) and the Yellow-faced Honeyeater (*Lichenostomus chrysops*). Both species left GMG, habitats in autumn and aggregated in RIGB habitats at this time (Mac Nally 1995*b*). These habitat-specific differences account for the significance of the habitat by strategy interaction term, which accounts for 21 % of the variation in the data (see table 3). Strategy accounts for over half of the variation (54 %, see table 3).

(*e*) *Habitat 'sharing' by itinerant strategists*

Resident species numerically dominated the forest and woodland habitats of central Victoria (see figure 2*a*). However, other temporal strategists are not

Table 3. *Repeated measures* ANOVA *of densities of spatial strategies* (*repeated measures on strategy and season factors, model 1*)

(MS denotes mean square; * indicates significant at the 5 % probability level; n.s. denotes not significant at the 5 % probability level; VC indicates the variance component. There are: 5 habitats (random factor); 3 strategies (fixed factor, stenotopy, oligotopy, eurytopy); and 4 seasons (fixed factor).)

factor	d.f.	MS	*F*-ratio	d.f. test	VC (%)
habitat (η)	4	354.3	1.01 n.s.	4, 15	≅ 0
plot within habitat (π)	15	351.0	—	—	3
strategy (ψ)	2	30,443.1	13.28*	2, 8	54
season (γ)	3	23.0	0.10 n.s.	3, 12	0
habitat, strategy ($\eta\psi$)	8	2292.1	18.74*	8, 165	21
habitat, season ($\eta\gamma$)	12	221.2	1.81 n.s.	12, 165	1
strategy, season ($\psi\gamma$)	6	224.2	1.37 n.s.	6, 24	1
three factor ($\eta\psi\gamma$)	24	164.3	1.34 n.s.	24, 165	2
residual (ϵ)	165	122.3	—	—	19

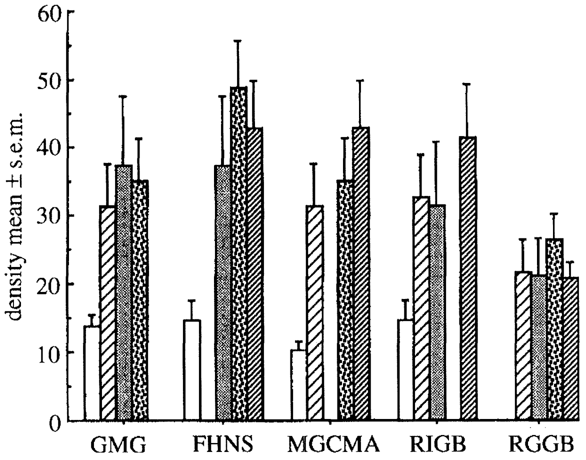

Figure 5. Habitat sharing by itinerant species. Total densities of all itinerant species found in any one habitat (e.g. GMG-abscissa) shared with each replicate of another habitat (see legend). Data are expressed as individuals per 10 ha: mean ± standard error (all $n = 4$). (▩) GMG; (▨) FHNS; (▧) MGCMA; (▦) RIGB; (□) RGGB.

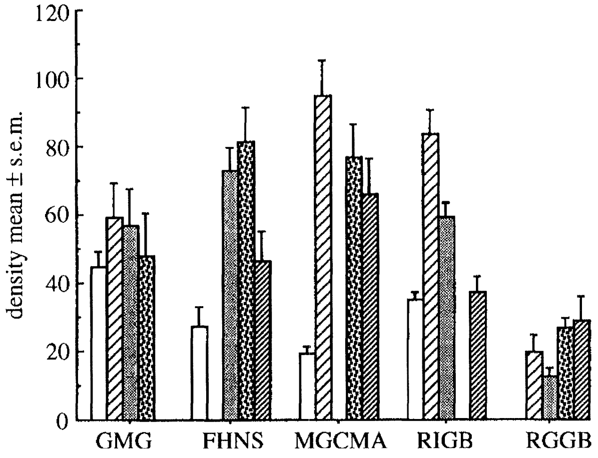

Figure 6. Habitat sharing by oligotopic species. Total densities of all oligotopic species found in any one habitat (e.g. GMG—abscissa) shared with each replicate of another habitat (see legend). Data are expressed as individuals/10 ha: mean ± standard error (all $n = 4$). (▩) GMG; (▨) FHNS; (▧)MGCMA; (▦) RIGB; (□) RGGB.

uniformly inconsequential, as was shown for habitat-specific analyses (§ 3*c*). Although regional migrants were comparatively rare in all habitats and seasons, there were relatively high densities of itinerant species in certain habitats in some seasons (see figure 3). The importance of itinerant species to an interpretation of the large-scale dynamics of bird communities is that they represent an identifiable element in which individuals clearly move among habitats. Thus itinerant species are indicators of the levels of sharing among habitats and the degree to which local processes might be affected by regional-scale movements.

To illustrate the interdependence of habitats via itinerant species, I calculated the total densities of all itinerant species occurring in a given type of habitat (call it the 'test' habitat; GMG, for example) that were found in each replicate plot of each other type of habitat. These data provide information on the degree to which two habitat types are 'connected' by the movements of itinerant species. Low total densities indicate that itinerant species do not 'share' two habitats to any great extent, whereas high total densities mean that there is much interchange among habitats. In the former, the two habitats may have the potential for essentially independent community dynamics in the absence of the impact of itinerant species, whereas high sharing negates the possibility of independent development of habitat-specific patterns of resource utilization.

Analyses of site-sharing by itinerant species indicated that itinerant species moved freely among all habitats except RGGB, with total densities usually exceeding 30 birds per 10 ha (see figure 5). This figure is approximately half of the density of residents occupying these habitats (see figure 3). Total densities of itinerant species in RGGB habitats comprised about 25% of the residents.

(*f*) *Habitat 'sharing' by oligotopic strategists*

Oligotopic species are similar to itinerant species because habitats 'share' them. An analysis of oligotopic species is needed as an analogue for the one conducted for itinerant species (§ 3*e*). Therefore I computed the total densities of all oligotopic species recorded in any of the replicates of the test habitat for each replicate of all other habitats. The results of this analysis showed clearly that the oligotopic species shared between MGCMA, FHNS and RIGB numerically dominated these habitat types (see figure 6). Sharing between these three habitats and GMG was less than among the three, but the total densities of oligotopic species shared between RGGB and the other habitats were relatively low.

(*g*) *Stenotopic residents*

For the purposes of the discussion, it will prove useful to illustrate the numerical significance of one component of the avifauna within each habitat type, the stenotopic residents. These strategists are ones that might be expected to have the potential for the development of differentiation because they are restricted to one habitat (among those surveyed) and occur year-round in that habitat in similar densities.

Stenotopic residents represented a minor component of the avifauna in all seasons in four of the habitats (GMG, FHNS, MGCMA and RIGB; see figure 7). Individuals of stenotopic, resident species represented an appreciable fraction of all birds in RGGB habitats alone. They comprised, on average, between 28% (winter) and 42% (summer) of the total individuals. Thus stenotopic residents are numerically insignificant in most habitats and are a minority in RGGB habitats.

4. DISCUSSION

(*a*) *The eight necessary conditions*

Of the eight necessary conditions for the development of specific community structure (see § 1), I can comment definitively on only three in relation to the bird communities occupying forests and woodlands of

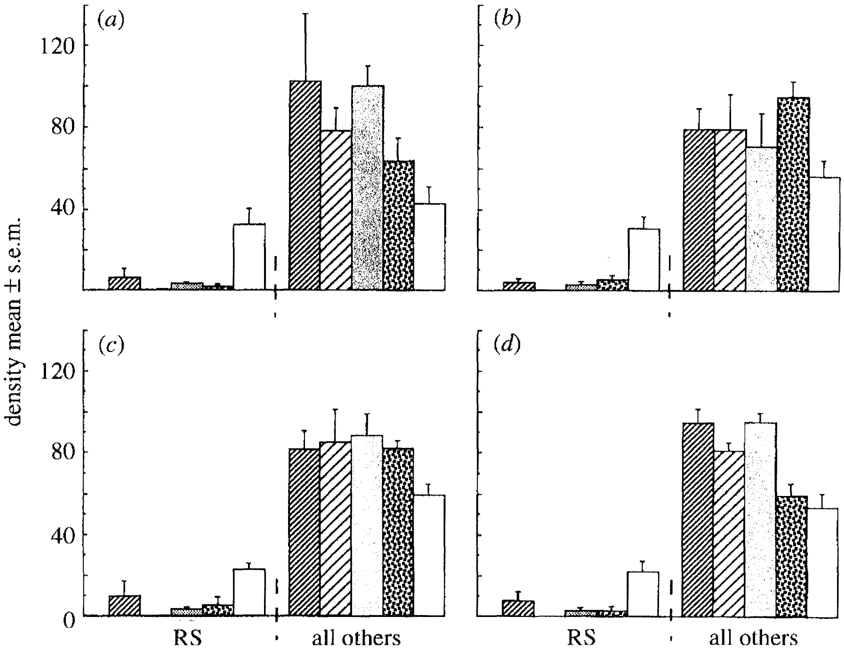

Figure 7. Total densities in each habitat of stenotopic residents (*RS*) and all other strategies (*all others*). (*a*) summer; (*b*) autumn; (*c*) winter; and (*d*) spring. Data are expressed as individuals per 10 ha: mean ± standard error (all $n = 4$). (▨) GMG; (▧) FHNS; (▩) MGCMA; (▣) RIGB; (□) RGGB.

central Victoria, namely, the co-occurrence (1), local recruitment (6) and closure (7) conditions. It is clear that none of these bird communities satisfies these conditions because of migrant and especially itinerant species. The latter move between different habitats on a seasonal basis, which means that their influence must vary at any given site through the year and also be transmitted among habitats (see figure 5). Although not numerically dominant in any habitat in a season, itinerant species nevertheless formed a significant fraction of the avifauna in several habitats in either the cooler (RIGB) or the warmer (GMG, MGCMA) seasons of the year (see figure 3). It might be argued that itinerant species have little overall impact because they mainly capitalize on 'bloom' resources such as nectar or seeds. Although this argument may apply to species such as the mostly nectarivorous Red Wattlebird (*Anthochaera curunculata*), other itinerant species such as the Yellow-faced (*Lichenostomus chrysops*) and White-naped (*Melithreptus lunatus*) Honeyeaters and the Striated and Spotted Pardalotes (*Pardalotus striatus and P. punctatus*) are mostly foliage searchers (Mac Nally 1994*a*) so that the bloom-resource argument does not readily apply to them.

Itinerant species clearly violate the closure criterion. In addition, at least many of the oligotopic (and eurytopic) resident species are unlikely to be strongly restricted to the habitats in which individuals are fledged. Given that oligotopic species dominate all habitats (see figure 2*b*) and that there is high sharing of oligotopic species among certain habitats (see figure 6), it seems unlikely that the closure condition will hold for oligotopic species either. As noted in § 3*g*, specific community structure would be most probable if communities consisted mainly of stenotopic resident species in which case the closure and co-occurrence conditions would be more likely to be satisfied. However, such species are a small component in all five habitats (see figure 7).

Dynamic variation in community structure is definitely underestimated in the current analyses because between-year variation has not been included (i.e. a year factor in addition to the habitat and season factors). Studies of the structure of continental bird communities extending over several to many years usually show substantial differences between the corresponding seasons of different years (for example, Pulliam 1986; Holmes 1990). I have recently recorded similar pronounced differences in the composition of a bird community between corresponding seasons in 1993 and 1994 at an MGCMA site near Melbourne (Olinda State Forest). For example, there was an enormous increase in the densities of most meliphagid honeyeaters (Red Wattlebirds and White-naped (*Melithreptus lunatus*) and Brown-headed Honeyeaters (*M. brevirostris*) in particular) in the winter of 1994 compared with 1993, but there were several other important differences including the occurrence in 1994 only of White-eared (*Lichenostomus leucotis*) and Crescent Honeyeaters (*Phylidonyris pyrrhoptera*), both of which mainly search smaller branches and twigs for invertebrates (Mac Nally 1994*a*). It would be worthwhile conducting a similar sampling program to the one described in this paper over several randomly selected years to quantify the sources of variability more completely. These data would help to circumscribe the extent to which mechanistic explanations of community structure could be tested in the field. Clearly, it would be fruitless to base an experimental program on one year's data without knowing the position of that year along the spectrum of annual variation for the habitats of this region.

I can make few direct statements about the other five necessary conditions. However, it may be useful to comment on some of the conditions as they apply to these bird communities. For condition 2 – resource constancy – variation in food availability is likely to be high in this region due to climatic variability. On average, every fourth year is comparatively dry during the normally wet August to November period (Mac Nally 1987). How between-year climatic variation affects variation in food production, especially of insects, fruit, seeds and nectar needs to be determined across the set of study habitats. Variation in at least some foods may be poorly correlated with rainfall. For example, the winter of 1994 was abnormally dry in most of eastern Australia yet the Mountain Grey Gums (*Eucalyptus cypellocarpa*) at Olinda State Forest flowered profusely.

For condition 3 – resource limitation – demonstrating chronic shortages of food resources is very difficult. Apart from problems of measuring absolute levels of food abundance (see Cooper & Whitmore 1990; Hutto 1990; Majer *et al.* 1990), Wolda (1990, p. 38) detailed the steps involved in determining relative food availability for a given species. If ecologically similar species perceive different relative availabilities due to dissimilar searching behaviour and/or visual acuity, then it will be hard to assess whether there are chronic shortages of food. Food requirements also need to be estimated to gauge whether food availability was likely to be limiting (see Abrams 1980*a*,*b*). Also, intraspecific rather interspecific interactions may have more impact on densities (see Chesson 1991), which, judging by levels of agonistic interactions, seems to be the case in at least some of the species (e.g. *Pachycephala* whistlers).

The fourth condition – environmental impartiality – is difficult to gauge but cannot be discounted over time scales comparable to generation lengths of most forest and woodland bird species (see Shugart 1990; Ornelas *et al.* 1993). Condition 5 – reflective recruitment – is one of the hardest aspects to quantify because of the complexity of factors involved. These include 'normal' fecundity rates (similar species may produce quite dissimilar standard clutch sizes), whether species produce multiple clutches, and especially the susceptibility of different species to nest predators. There is a rising recognition that much of community theory as applied to forest birds may be largely irrelevant because of high levels of nest predation or nest parasitism (see for example, Martin 1988; Small & Hunter 1988; Wilcove & Robinson 1990). If this were generally true, then condition 8 – saturated environments – would be violated too. Wiens (1989, see chapter 3) analysed how processes other than interspecific competition can deflect community structure from a 'predicted' state based on competition theory to alternative states, citing such factors as predation on adults and on nests, parasitism and brood parasitism, commensalism and history as potentially influential. To this list should be added, at least for large, unconstrained geographic areas, species-specific, seasonal responses to climatic and resource availability.

In summary, eight conditions need to be satisfied for interspecific interactions to lead to well-defined ecological differentiation within communities of birds at the local scale (tens of ha, say). Each condition was considered in light of the specific information reported from this study of the avifaunal dynamics of five of the main forest and woodland habitats of the central Victorian region and additional observations made on comparable temperate zone forests from other continents. Field workers must be prepared to evaluate explicitly the degree to which their study systems meet these necessary conditions before interpreting function and structure as responses to local ecological interactions. It seems unlikely that these eight conditions will be satisfied in almost any continental context (or even on large islands such as Borneo, New Guinea or Tasmania), and even if they are, then these situations would be atypical and unrepresentative of continental avifaunas.

(*b*) *Large-scale dynamics and community structure*

Although there is increasing recognition that bird communities are dynamic assemblages, many of these conclusions have been drawn from small-scale studies (i.e. tens of ha) in which workers monitor the ebb and flow of the constituent species through the year or between years (see for example, Herrera 1978; Holmes 1990; Tomialojc & Wesolowski 1990). The current study places community dynamics in a broader regional context leading to a clearer understanding of the ways in which bird communities are structured in relation to the individual dynamic strategies of species. For example, the key issue of the proportions of stenotopic resident species (see figure 7) can be resolved for many habitat types simultaneously. The small fraction of such species in all habitats almost immediately precludes the possibility that ecological differentiation, such as it is, will be derived from habitat-specific processes. Like most ecological studies, the study domain (the survey line) was defined at an arbitrary spatial scale that was largely determined by logistic feasibility. At even larger spatial scales, other arboreal habitat types such as mallee and mulga would need to be included and the perceived degree of stenotopy would be even less. Thus it is important to recognize the scale dependence of estimates of habitat specificity (these are sample estimates), and those reported by Mac Nally (1995*b*) most probably overestimate the habitat specificity of many species.

According to niche theory, the ecological characteristics of coexisting species should be moulded by coevolutionary accommodations (for example, MacArthur & Levins 1967; Roughgarden 1974, 1979; Chesson 1988; Loreau 1989, 1992). I noted at the outset that one of the main causes of problems in understanding ecological communities, and especially function within communities, is an inadequate attention to dynamics. The complexity of changes in the composition of forest and woodland bird communities in terms of the dynamic strategies of species almost certainly negates the potential for the development of small-scale functional differentiation among species. If the ecological characteristics of continental biotas are indeed fashioned at landscape or regional scales, as many workers now believe (for example, Rice *et al.* 1980; Ricklefs 1987; Dunning *et al.* 1992; Ricklefs &

Schluter 1993), then it seems clear why evidence of clear ecological differentiation at the local scale is not easy to document. The rapid growth of guild-oriented studies (Hawkins & MacMahon 1989) probably reflects observational data in which ecological similarities within communities are more pronounced than the consistent differences predicted by niche diversification theory (see Tokeshi 1993). Thus trying to account for diversity at the local scale via niche theory (and thus local or small scale processes) misses the evident point that, at least for continental bird communities, this is an entirely inappropriate spatial scale.

Modelling paradigms of interspecific interactions at multiple spatial scales show that the coexistence of ecologically 'identical' species can be mediated by dispersal within heterogeneous landscapes. Many of these models employ essentially classical competition dynamics at the local scale (e.g. Danielson 1991, 1992; Palmer 1992; Tilman 1994) yet the competitive exclusion implicit in these models does not necessarily emerge at the larger scales. That is, even were Lotka-Volterra dynamics relevant at local scales, environmental heterogeneity coupled with migration and dispersal across landscapes frequently prevent the large-scale exclusion of similar species in model communities. Given that these features – heterogeneous landscapes and species-specific regional dynamics – characterize continental bird communities (e.g. Colwell 1993; Ornelas *et al.* 1993; Blake *et al.* 1994), it is not surprising that similar species should frequently co-occur. To the contrary, it would be surprising were ecological differentiation to emerge from small-scale competitive interactions.

Community dynamics between seasons and among years and the extent to which populations communicate with conspecific populations in other habitats and places govern the potential for community structure (including resource partitioning) to develop. Thus local diversity in continental bird communities is unlikely to be regulated by competitive processes irrespective of whether population densities are constrained by other factors such as brood parasitism or predation on adults. Such communities will be Gleasonian (species acting more or less independently) rather than Clementsian (integrated, coevolved communities) in nature. Local diversity at any time appears to be determined by a complex relation between the available regional pool of species potentially able to occupy a location, idiosyncratic habitat requirements and large-scale dynamics of individual species, resource irruptions and habitat architectures.

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