Ecology, 67(4), 1986, pp. 1073–1085

TESTS FOR SIMILARITY AND CONVERGENCE OF FINCH COMMUNITIES[1]

DOLPH SCHLUTER
Department of Zoology, University of British Columbia, Vancouver, British Columbia V6T 2A9 Canada

Abstract. Convergence at the community level occurs when whole groups of organisms become more similar than their ancestors in a similar environment. I suggest a method for indirectly assessing community convergence, and apply it to several characteristics of finch communities in different habitats worldwide. The method is based on the analysis of variance, and has several advantages over other indirect tests for convergence. Advantages include: (a) convergence is tested by comparing the variance between replicate communities within habitats to the variance between habitats, using a large and representative sample of habitat types; (b) the method estimates degree of convergence, a useful index for contrasting convergence of different community traits; (c) historical constraint on community convergence may be viewed as an additional component of total variation in the community character, and its importance can be estimated and compared with the effect of habitat type. The method revealed significant convergence of finch species number, mean finch size, mean finch shape (body size relative to beak size), and standard deviation in shape. Standard deviation in finch size may also have been convergent, but the pattern was not significant. From nearly 30 to >60% of the variability in these community traits was attributable to an effect of similar habitat type. Significant variability in one trait (mean shape) was also attributable to geographic region, apparently an effect of differences between regions in the phylogenetic origin of finches present. Hence, historical factors appear to have constrained convergence, but only in one of the five finch community traits.

I also suggest some methods to evaluate community similarity, and apply these to four of the five finch community traits (species number excepted). Similarity of communities within habitat types was unrelated to the degree of convergence. For example, finch communities within habitats were significantly similar in only one convergent trait, mean size. Mean shape, also convergent, was significantly different between communities within habitats. Similarity, as defined here, indicates that sizes of individual species within communities are nonrandomly spaced. Interspecific interactions may thus be involved in the convergence of at least one trait, mean finch size.

Key words: coevolution; community-level convergence; community similarity; community structure; finches; guild structure; null models.

INTRODUCTION

The hypothesis of convergence is that under similar environmental conditions, species or groups of species have become more similar in certain characteristics than their ancestors (Cody and Mooney 1978, Orians and Paine 1983). Numerous cases of convergence of individual species have been reported (Karr and James 1975, Orians and Solbrig 1977, Cody and Mooney 1978). For example, many species of plants and animals occurring in the monte desert of Argentina are morphologically and ecologically analogous to unrelated species in the Sonoran desert (Orians and Solbrig 1977).

We are less certain whether guilds or entire communities of organisms have converged in some traits (e.g., species diversity) (Ricklefs and Travis 1980, Orians and Paine 1983, Blondel et al. 1984, Lawton 1984). The problem is of current interest for two main reasons. First, community convergence is an important aspect of the more general hypothesis that characteristics of organisms are predictable from features of their environment. Second, whereas convergence at the level of species can often be explained as an effect of similar resources, convergence of community properties may in addition indicate the importance of interspecific interactions such as competition (Cody 1974, Orians and Paine 1983, Lawton 1984).

Unfortunately, community convergence can rarely be assessed directly, since the ancestral characteristics are usually unknown. The task of assessing community convergence indirectly is exacerbated by two problems. The first is the absence of general criteria. For example, assessments of convergence between two or more communities often rely heavily on measurements of community similarity (Pianka 1973, Karr and James 1975, Fuentes 1976, Orians and Solbrig 1977, Cody and Mooney 1978, Ricklefs and Travis 1980, Lawton 1984). A high degree of similarity may indicate convergence, but in general there is no straightforward relationship between similarity and convergence. Communities that are highly dissimilar in some trait may nonetheless have converged in that trait with respect to their ancestors; conversely, similar communities may merely have failed to diverge. One potential solution to this first problem is to compare attributes of communities in a similar environment to "control" communities in a different environment (Fuentes 1976, Mares 1976, Or-

---

[1] Manuscript received 7 June 1985; revised 8 November 1985; accepted 14 November 1985.

ians and Solbrig 1977, Cody and Mooney 1978, Blondel et al. 1984), a technique which has not been exploited to full advantage (Blondel et al. 1984).

The second problem is that the indirect assessment of convergence is usually qualitative. The lack of a quantity for convergence makes it difficult to compare the degree of convergence exhibited in different traits or different groups of organisms. The lack of such a quantity also makes it difficult to compare the statistical effects of similar environments on community attributes (convergence), with the effects of alternate factors, such as phylogenetic origin.

In this paper I introduce some general criteria for indirectly measuring and testing community convergence. I then use the method to assess convergence in species richness and morphological properties of granivorous finch communities in similar habitats on various continents. The approach I advocate is based on the familiar analysis of variance. Observed variation among finch communities in each trait is partitioned into components, including habitat effects and historical effects. The importance of the two causal components is then estimated and compared for different community characters. I also suggest some ways to measure and test community similarity. I compare similarity and convergence of each trait in the finches, to test whether the two measures are related.

In this study, convergence at the level of individual species is already known to be present: the term "finch" applies to small, seed-eating birds with relatively heavy, conical beaks in at least four continental families (Fringillidae, Emberizidae, Ploceidae, and Estrildidae) (Newton 1973). For simplicity, unless otherwise mentioned, "convergence" hereafter refers to convergence at the level of guilds or "communities" of organisms.

TESTS OF SIMILARITY AND CONVERGENCE

Convergence

Convergence has occurred when different communities in similar environments are more similar than their ancestors (Cody and Mooney 1978, Orians and Paine 1983). In most studies, the characteristics of ancestral communities will not be known. However, convergence can be inferred indirectly if a range of habitat types (or other environmental states) is available, and if different communities of a given habitat type are largely independent (e.g., exist on different continents).

Fig. 1 illustrates how convergence may be detected. Fig. 1A presents a hypothetical ancestral condition, with large differences between communities from different continents, and no initial differences between communities in different habitats within continents. Optimum values for the community character are different in the two habitats, and through time the communities will converge to correspond more closely to these optima. The result is a difference between habitat types in the average community value (Fig. 1B).

Thus, with the sequence A → B (Fig. 1) detecting convergence is equivalent to detecting a difference between habitats in average observed community value, a simple problem in analysis of variance. Formally, the observed value Y of community j in habitat type i can be thought of as the sum of three components,

$$Y(ij) = \mu + \tau(i) + \epsilon(ij), \qquad (1)$$

an overall mean, a fixed deviation due to habitat type, and a random error. Convergence has occurred when not all the $\tau(i)$ are zero. This is evidenced by a significant habitat effect in a fixed effects model ANOVA, or nonparametric alternative, with communities (not individual species) as replicates.

Note that parallelism produces the same result. Ancestral communities may change to correspond more closely to habitat optima (Fig. 1C), but initial differences between communities in the same habitat are maintained throughout. Parallelism is sometimes included within the definition of convergence (Cody and Mooney 1978). While I feel it would be useful to distinguish between parallelism and convergence, indirect tests will not allow us to do this. Methods presented here thus assess parallelism and true convergence combined. Though strictly incorrect, for convenience I refer to the combination as "convergence."

The amount of convergence may be large or small, and so it is useful for comparative studies to have a quantity or index of convergence. A simple index is

$$C = \alpha^2/(\alpha^2 + \sigma^2), \qquad (2)$$

where σ^2 is the pooled variance of the community character within habitat types, α^2 is the variance among treatment means, and C is the fraction of the total variance in Y which is among habitats. C can vary between 0 and 1. $C = 1$ corresponds to complete convergence, and $C = 0$ to an absence of convergence. A significant habitat effect on the community character indicates that $C > 0$, i.e., some convergence has occurred.

Historical effects

Complete convergence may be constrained by phylogeny or other historical differences between communities. This pattern is illustrated in Fig. 1B, where community differences between continental groups may persist regardless of habitat. In many applications a factor incorporating some of these historical differences can be identified (e.g., phylogenetic origin, or continent), and the contribution of this factor to total variance in the community character can be estimated and compared with the effect of habitat type.

Expanding Eq. 1, the value of the variable Y in community k is the sum of an overall mean (μ), a fixed habitat deviation (τ), a fixed deviation resulting from the historical factors (κ), and a random error:

$$Y(ijk) = \mu + \tau(i) + \kappa(j) + \epsilon(ijk). \qquad (3)$$

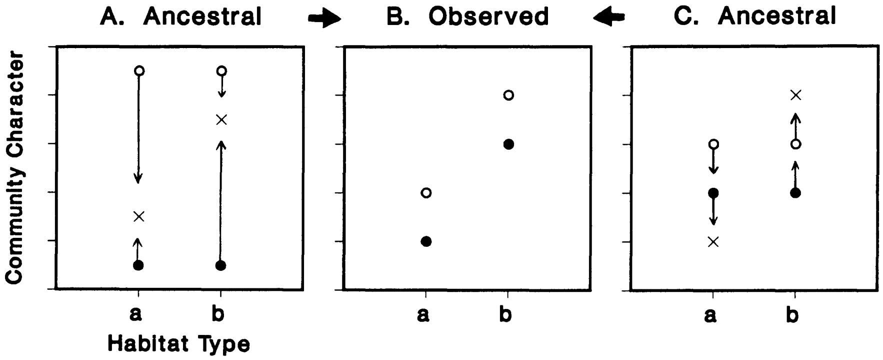

FIG. 1. Historical sequences leading to an association between habitat type and average value for the community character. ○ and ● represent two independent groups of communities, each existing on a separate continent. A and C are alternative ancestral conditions leading to B. × indicates a hypothetical optimum value for the community character in each habitat type. → indicates magnitude and direction of change of the character in the ancestral community.

This equation can be modified to incorporate interactions between τ and κ, nested variables, and so on (Sokal and Rohlf 1981). As before, the hypothesis of convergence is supported if there is a significant habitat effect on the community variable. Standard methods similarly test for a significant effect of the historical variable.

In the case of Eq. 3, a modified index of convergence is

$$C = \alpha^2/(\alpha^2 + \beta^2 + \sigma^2), \tag{4}$$

where α^2 is the variance among habitats, and β^2 is the variance among historical groups. As before, C is the fraction of the variance in the community variable which is among habitats. The importance of the historical variable is similarly computed as

$$H = \beta^2/(\alpha^2 + \beta^2 + \sigma^2), \tag{5}$$

where H measures the fraction of the variance in Y attributable to identified historical factors. Both C and H vary between 0 and 1.

Similarity

Though convergence is of primary interest, similarity measures are useful in addition. Below, I suggest some measures of similarity that can be applied to different communities in the same habitat type (or other environmental state). Similarity can also be measured between communities in different habitat types, but in this case measures of convergence are more useful. Similarity and convergence are later compared for different finch community traits.

A variety of measures of similarity are conceivable. For example, a community variable may be a mean of a property of the individual species present (e.g., mean body size), and absolute difference in mean size between two communities is a simple measure of similarity (or distance) between them. However, an alternate similarity measure is often desired, one allowing a direct evaluation of whether communities are more similar (or more different) than expected by chance. When community means are compared, an appropriate statistic for similarity is the F ratio of mean squares between and within communities, as in a random effects model ANOVA (see Sokal and Rohlf 1981), where replicates within communities are the individual species values. The expected values of the numerator and the denominator of F are equal, under the null hypothesis that the observed means are based on random samples from the same distribution. If F is much larger than 1, then the communities are significantly different. Conversely, if F is close to zero, then the communities are improbably similar. Community similarity is thus tested using a two-tailed F test (Sokal and Rohlf 1981) in contrast to the one-tailed tests used in analysis of variance.

The F statistic of similarity is computed as for ANOVA, but the statistical model is subtly different (Snedecor and Cochran 1967:294). Here, F measures the intraclass correlation, the extent to which individual species occurring in the same community are alike or unalike in the character of interest (Fisher 1948, Snedecor and Cochran 1967). The intraclass correlation between species in the same community is positive when the communities have different sample means ($F > 1$), and it is negative when the communities have similar means. In the body size example, similar community means indicate that species within communities are nonrandomly (widely) spaced along the body-size axis. Significant similarity of communities would thus suggest an effect on the community variable of competitive interactions between species of the same size, or of mutualism between species of different size. Similarity analysis is therefore one method to evaluate whether species interactions have been involved in producing the observed level of convergence.

Analogous measures of similarity can be determined for other community attributes, not necessarily means. For example, standard goodness of fit or contingency tests based on χ^2 can be modified to test for a significant

TABLE 1. Number of communities used in the present analysis, by habitat type and geographic region.

Habitat	Region*				
	NA	SA	EUR	AFR	AUS
Lowland tropical wet forest		1			1
Lowland tropical open grassland		2		1	1
Tropical savanna woodland		1		1	
Tropical thorn steppe		1		1	1
Mediterranean scrub	1	1	1	1	1
Warm temperate desert	1	1			
Warm temperate grassland	1	1			
Cold temperate desert		1	1		
Temperate deciduous woodland	1		1		

* Regions are NA (North America), SA (southern Central and South America), EUR (Europe and west Asia), AFR (Africa) and AUS (Australia and southeast Asia).

similarity simply by employing the lower tail of the χ^2 distribution (Fisher 1936 gives an interesting example). The general procedure incorporates many other tests of similarity that have been used. For example, similarity of two communities in the cumulative distribution functions of a species trait such as body size (i.e., a small value for the Kolmogorov-Smirnov D) is essentially a test of species-for-species matching (cf. Lack 1968, Cody 1974, Karr and James 1975, Ricklefs and Travis 1980).

METHODS

Species lists and habitats

The above procedures were applied to measuring similarity and convergence of finch communities in habitats of various geographical regions. Species lists are given in the Appendix. Lists were obtained chiefly for the nonbreeding season, because finches are generally most granivorous then, and natural selection on beak and body size is most frequent in the nonbreeding season (Boag and Grant 1981, Price et al. 1984, Schluter and Smith 1986). This choice of season affects lists primarily for the north-temperate regions, where many species are migratory. In other regions, I occasionally used breeding lists when these were the only ones available (e.g., monte desert).

The lists are not exhaustive for the particular habitats. First, lists are based mainly on individual surveys from specific locations within each habitat type and not on the entire habitat. Hence they represent estimates of local diversity for different regions. I used distribution maps to estimate local diversity for one habitat type (cold temperate desert). However, the number of species is low in both lists for this habitat (Appendix), and unlikely to be greatly inflated. Lists for different communities were compiled by different persons, and they may not be equally exhaustive. This variation no doubt contributes to random variation between communities in their characteristics.

Second, not all species that were observed in the specified habitats are listed. Where information provided by the various sources allowed, I excluded rare species, and species that clearly preferred other habitats over the one of interest. For example, *Euplectes afer* occurs in tropical savanna woodland in northern Ghana, but Greig-Smith (1976) lists it as preferring other habitats. Similarly, *Acanthis flammea* is atypical of English oak woodland (Peterson et al. 1983, F. Vuilleumier, *personal communication*) and I did not include it, even though Lack and Venables (1939) list it as present.

Finally, where information allowed, I excluded species that were not granivorous. For example, Orians (1969) lists species of the Emberizidae found in forest sites in Costa Rica, and their diets; those that did not feed on seeds were excluded from my analysis. Similarly, the weaver *Malimbus rubriceps* occurs in tropical savanna woodland of northern Ghana (Greig-Smith 1976). However, Hall and Moreau (1970) note that the species is insectivorous, and I did not include it.

A test for convergence assumes that similar environments are present in different geographic regions. Finch communities were grouped on the basis of habitat type. In some cases sites in the same habitat in different regions were shown to be similar by the authors of species lists (e.g., mediterranean scrub, Cody and Mooney 1978; tropical savanna woodland, Fry 1980; warm temperate desert, Orians and Solbrig 1977). In other cases I used general habitat classes to group communities (e.g., Logan 1968, McGinnies 1979, Bourlière 1983). The habitat classes that I used are quite distinct (Table 1), and while sites within each habitat type are not identical, they should be much more similar to each other than to sites in other habitats. All but the weakest forms of convergence should therefore be detectable in the present analysis.

In all, lists were compiled from 24 locations involving nine habitat types and five geographic regions (Table 1). Over half of the 45 possible habitat-by-region combinations are represented. Certain combinations are absent simply because all habitats do not occur on all continents. For other combinations I was unable to obtain comparable species lists from the nonbreeding season. Finally, finch species lists are not independent across regions in some habitat types (e.g., lists from cold temperate desert in North America include species

TABLE 2. The percentage of species in finch communities belonging to the four different families, by region. Allocation of species to families follows Morony et al. (1975).

Family	Region*				
	NA	SA	EUR	AFR	AUS
	Percentage of finch species				
Emberizidae	87	100	29	10	
Fringillidae	13		71	17	
Estrildidae				33	100
Ploceidae				40	
No. finch species	15	35	7	30	6

* Regions defined as in Table 1.

found in Europe-western Asia sites). In such cases I used the site from one geographic region only. No bird species occurred in more than one region, although a few were common to different habitats within a region. Four finch families were represented, and their frequency by region is given in Table 2.

Community characteristics

I compared communities with respect to species number and morphological traits. Morphological measurements were taken from museum specimens, mainly at the American Museum of Natural History in New York. Some additional specimens were measured at the Museum of Vertebrate Zoology, University of California, Berkeley. For each species, five characters were measured on 10 male specimens collected from sites as close as possible to the locations used in the present study. The characters are wing length, tarsus length, beak length, beak depth, and beak width, all in millimetres. These were measured as described in Schluter and Grant (1984*a*), except for beak width, which was measured at the anterior end of the nares.

All characters were ln-transformed and averaged within species by locations. The five traits were then reduced to two principal components using the covariance matrix from all species combined. The five original variables load positively and roughly equally onto the first component, PC1; therefore this is a general size variable (Pimentel 1979). Four traits load onto the second component, PC2: wing and tarsus length positively, and beak depth and width negatively. Therefore PC2 is a shape variable, specifically, body size relative to beak stoutness. PC1 and PC2 account for most of the variance among species (63 and 25%, respectively), and hence PC3–PC5 were not used.

Four community variables are based on these measurements: mean size (PC1), mean shape (PC2), and standard deviation (SD) in size and shape. Including species number, five variables were compared among communities.

Statistical analysis

Similarity.—I computed similarity indices, F, for community morphology within habitat types using standard ANOVA computations. For mean size (PC1) and mean shape (PC2), F was based on the species values. For standard deviations (SDs), I used $X(i) = |Y(i) - M|$, where $Y(i)$ is the size or shape of species i, and M is the median of $Y(i)$ in the particular community. The comparison of mean squares based on the variable X is a two-tailed Levene's test for similarity or differences in community mean dispersion (see Schultz 1983). Significance levels were based on the F distribution, but nonparametric tests (two-tailed Kruskal-Wallis) gave essentially the same results. Similarities were not computed for species number, in the absence of a suitable statistical model governing species presence/absence.

Convergence.—Significance levels in tests for convergence of finch communities were based on standard ANOVAs using community values as replicates. Both one- and two-way analyses were performed, the first including the factor habitat type, and the second including both habitat type and geographic region. For the four morphological variables I carried out both weighted and unweighted ANOVAs in each case. Weighting accounts for the fact that estimates of community morpology are computed from different numbers of species in the different communities, resulting in different standard errors. Estimates of morphological traits are weighted by the number of degrees of freedom on which they are based: n for means, and $n - 1$ for SDs, where n is the number of species present (e.g., Sokal and Rohlf 1981:407). An effect of this weighting is that the index of convergence is more strongly influenced by the characteristics of communities and habitat types with the largest numbers of species. This effect is not always desirable, particularly if one considers the observed values of the community traits to be the true values, and not merely estimates (e.g., Blondel et al. 1984). For this reason I present results from both the weighted and unweighted analyses.

Community standard deviations in size and shape were ln-transformed prior to analysis of variance (Sokal and Rohlf 1981). Community values for number of species, mean size, and mean shape were left untransformed. The resulting community values conformed reasonably well with assumptions of ANOVA, but as a precaution, significance levels were checked in all cases using randomization (Sokal and Rohlf 1981: 787). Randomization involved reassigning observed community values randomly to habitat types 500 times, maintaining the number of values in each habitat type. The sum of squares within habitats (SSW) was computed for each of the 500 combinations, providing a null distribution for this variable (the total sum of squares is constant). Significance is judged by the fraction of SSW values lying below the observed quantity. In the finch communities such randomization tests gave essentially the same results as standard ANOVAs, and only the ANOVA results are presented here.

Two communities were available from South American tropical open grassland (Table 1), and their characteristics were similar. Since the two sites may not be independent, I used the average of their characteristics in tests of convergence. Results were similar when one or the other community was used instead of their average.

RESULTS

Similarity

Finch communities within habitats tended to be more similar in mean size (PC1) than expected by chance (Table 3). F values in mean size were <1 in six of eight

TABLE 3. Similarity of finch communities within habitat types. Size is measured by PC1, shape by PC2.

		F values‡			
		Mean		SD	
Habitat	df	Size	Shape	Size	Shape
Tropical wet forest§	...	...	...	...	...
Tropical open grassland	3,14	0.42	4.91*	1.45	3.74†
Tropical savanna woodland	1,21	0.03	0.74	0.40	1.32
Tropical thorn steppe	2,15	0.06	8.74**	0.93	0.48
Mediterranean scrub	4,15	0.24	2.24	0.48	0.13
Warm temperate desert	1,11	0.69	0.01	3.26	0.05
Warm temperate grassland	1,8	1.47	6.64†	0.10	0.20
Cold temperate desert	1,3	3.21	0.89	0.74	0.03
Temperate deciduous woodland	1,3	0.38	1.13	1.11	0.03
Combined	14,90	0.28**	2.88**	0.83	0.85

† $P < .10$, * $P < .05$, ** $P < .01$, two-tailed F tests.

‡ Values are for the ratio of mean squares between and within communities. df are the number of degrees of freedom in the numerator and denominator, respectively.

§ Two sites are available for tropical wet forest (Appendix), but one of these has no finch species.

comparisons, although none was significant ($P > .10$). Significance levels from the different habitats can be combined in an overall F test, assuming that the individual tests are independent. This assumption is reasonable, since values of mean size from different habitats in the same geographic region are uncorrelated (see Historical Effects). The combined F was computed as in a nested ANOVA, with communities nested within habitat types, using the individual species values as replicates. The resulting F value was small (0.28) and highly significant ($P = .009$), indicating strong similarity in mean finch size of communities within habitat types (Table 3).

A different result was observed for mean finch shape (PC2), where communities tended to be different (Table 3). Five of eight F values exceeded 1, and three of these were significant at level .10. One F value was very small (warm temperate desert), but not significant. F was large (2.88) when the different habitats were combined in an overall test, indicating significant differences in mean finch shape of communities within habitats.

Communities were not consistently different or similar in standard deviation of size and shape (Table 3). One F value for SD of shape was significant at the .10 level, but F values computed from the combined data were not significant for either variable ($P = .63$ and .60, respectively).

Convergence

Species number was significantly convergent (Table 4), as illustrated by a conspicuous relationship between mean number of species and habitat type (Fig. 2). Number of species was highest in tropical savanna woodland sites in Africa and South America, while values were lowest in tropical wet forest, in cold desert, and in temperate deciduous woodland. Average numbers of species in other habitats were intermediate, ranging between four and six species. Number of species was highly variable between sites in two of the habitats, tropical thorn steppe and mediterranean scrub.

Mean finch size (PC1) was also strongly convergent (Table 4). In this analysis 77% of the observed variability among communities was among habitat types. The largest value for mean size was observed from a single community in tropical wet forest (Fig. 3). Large average values were also recorded from another forest habitat, temperate deciduous woodland, and from cold temperate desert and mediterranean scrub. Smallest values of mean size were observed from sites in tropical savanna woodland, tropical thorn steppe, and warm temperate grassland.

Convergence in mean finch shape (PC2) was detected (Table 4), even though communities within habitats were significantly different in this variable (Table 3). This result supports the earlier conjecture that similarity measures may be misleading as a criterion for community convergence. SD of shape was also significantly convergent, with habitat type explaining at least 55% of the variation among finch communities. No significant convergence was detected in SD of size, although C values were quite large ($P = .06$).

Historical effects

Certain aspects of finch communities might be peculiar to geographic regions, owing to differences in the phylogenetic origin of finch species present (Table 2) and their biogeographic history. Some regional effects are suggested in Fig. 2: Australia and southeast Asia are slightly depauperate in finches in several habitats. Table 5 summarizes the statistical effects of habitat (C) and geographic region (H) on the five community variables. Design in both weighted and unweighted analyses was a two-way fixed effects ANOVA (cf. Eq. 3), with a single community value per available treatment. With this design it is not possible to test for interactions between habitat and region; interactions are included instead in the error term.

C values in all traits were somewhat lower in the two-factor model than in the earlier analysis where habitat type was the single factor (Table 5). Upward biases in estimates of convergence when geographic region is not included are a consequence of an association between habitat type and geographic region (Table 1). For example, while temperate oak woodland sites were available from North America and Europe, tropical savanna woodland sites were from Africa and South America. The association between factors causes some of the effects of geographic region on the community trait to appear as effects of habitat type, when region is not included in the model. This problem would not be corrected simply by a more complete sampling of regions and habitats (Table 1), because climate and habitat types are generally different between regions. The inevitability of associations between habitat and region illustrates another advantage of the ANOVA approach: as in regression, ANOVA can tease apart the separate influences of the different factors.

Though lower, *C* values for number of species, mean size, and SD shape remained large and significant (Table 5), supporting the hypothesis of convergence. Each of these traits was more strongly affected by habitat than by region. This was particularly true of mean size, where habitat explained >60% of the variation among communities, and where the effect of geographic region was negligible. Small effects of region may have been present in number of species and SD of shape (Table 5), but these are not significant with my sample sizes. Like number of species, SD of shape tends to be low in the region of Australia-southeast Asia.

A different situation held in mean finch shape (PC2), where the effect of geographic region was dominant (Table 5). Convergence was also detected, although the habitat effect was significant only in the unweighted analysis ($P = .06$ in the weighted analysis). The strong effect of geographic region implies that substantial differences between continents in mean finch shape are maintained regardless of habitat type. Such a pattern is indicated in Fig. 4. For example, values for mean shape in Australia-southeast Asia are low and do not overlap with those from other regions. Finch communities in this region are dominated by the Estrildidae, which characteristically possess a small body size relative to stoutness of the beak (e.g., Goodwin 1982).

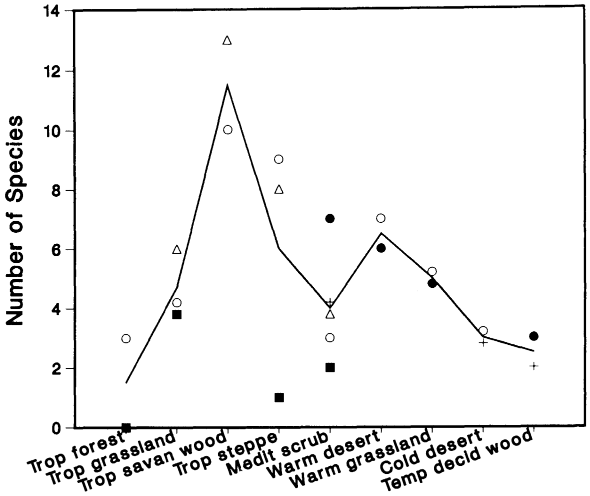

FIG. 2. Finch species number in relation to habitat type. Solid line connects average values of the different habitat types. Symbols indicate communities from different geographic regions: ● North America, ○ Central and South America, + Europe and western Asia, △ Africa, and ■ Australia and southeast Asia. Habitat types named in full in Table 1.

TABLE 4. Convergence among communities of finches. Size and shape are as measured by PC1 and PC2, respectively. *C* can vary between 0 and 1, where 1 indicates complete convergence.

	Convergence index (*C*)	
Community variable	Unweighted	Weighted
No. species	0.54*	...
Mean size	0.77***	0.77***
Mean shape	0.42*	0.43*
SD of size	0.43	0.42
SD of shape	0.55*	0.57*

* $P < .05$, *** $P < .001$.

Standard deviation in finch size was not significantly convergent (Table 5). However, *C* values were positive and quite large ($P = .09$ and $.07$ for unweighted and weighted analyses, respectively), suggesting that some convergence may nonetheless be present in this variable.

DISCUSSION

Procedure

The components of variance approach suggested here for testing convergence has some advantages over other indirect tests. First, it provides a quantitative measure of convergence, *C*. This measure allows succinct comparison of the degree of convergence in different community variables, variables which might otherwise be incommensurate (e.g., mean finch size and number of finch species). The measure would also allow comparison of convergence patterns between different studies and study organisms on a similar scale.

Second, while some studies have compared communities of a given habitat type to alternate communities in other habitats (Fuentes 1976, Mares 1976, Orians and Solbrig 1977, Cody and Mooney 1978, Blondel et al. 1984), usually only one or a small number of alternate communities has been used. Here, ANOVAs essentially compare communities of each habitat type with many alternate communities, and the results are less dependent on the choice of alternates. Indeed, a representative sample of communities and habitats is essential for the ANOVA method when degree of convergence is estimated.

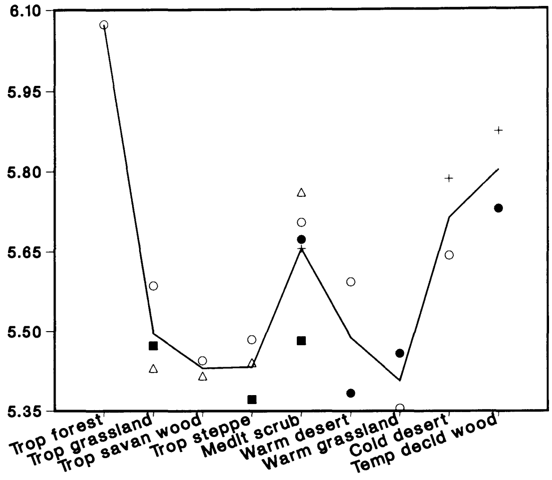

FIG. 3. Mean finch size (PC1) in finch communities in relation to habitat type. Solid line connects average values of the different habitat types. Habitat types named in full in Table 1; symbols as in Fig. 2.

Third, the criterion for convergence based on components of variance is more powerful than previous ones. For example, Blondel et al. (1984) employed the criterion that all communities within a habitat type should be more similar to each other than any is to communities in a different habitat type. It can be shown that *C* must be at least 0.78 to satisfy this criterion. A relaxed version of this criterion, one demanding only that variance within habitats be less than the variance between habitats (e.g., Fuentes 1976), still requires that *C* exceed 0.50. Clearly, in many situations convergence will be present, as indicated by a significant value of *C*, yet other criteria will not detect it.

Fourth, the ANOVA method allows us to consider quantitatively factors other than habitat type that might determine value of the community variable. Even if these other factors are not directly of interest, failure to consider them may lead to biased estimates of convergence (i.e., Table 4). Previous authors have noted that the effects of similar habitat type may be difficult to distinguish from those of similar phylogenetic origin (e.g., Blondel et al. 1984). In many situations the present method will be the appropriate one for identifying the separate roles of these two factors.

But like other approaches, the ANOVA method provides only an indirect test of convergence, and as a result it possesses inevitable shortcomings. First, though convergence is detected as differences among habitats in average community value (Fig. 1B), the same habitat effect could result from a wide range of initial differences between ancestors (Fig. 1A). *C* can therefore underestimate the amount of true convergence that has occurred. This problem is most severe when differences between habitats in the optimum value for the community character are small.

Second, the procedure assumes that habitats of the same type in different geographic regions are identical in their effect on the characters of interest. Departures from this assumption are likely, producing a greater variance among communities within a habitat type, and a corresponding underestimation of convergence using *C*. If geographic regions are consistently different in some ecological features (e.g., if continents differ in all habitats in the types of foods or competitors present), then *H* may be similarly inflated.

Third, the ANOVA approach provides an overall test of convergence, but it does not address events in any particular habitat type. Communities may be more similar in some habitats than others, but we cannot test whether they are "more convergent" in some habitats without a knowledge of ancestral conditions.

Finally, the magnitude of *C* will be influenced by the range of habitat types investigated, and their scale of definition. For example, results of analyses comparing different habitat types will differ from results when microhabitats within a given habitat type are compared instead. Similarly, results may depend on the taxonomic diversity of species considered, in effect the variability of $\kappa(j)$. This sensitivity to characteristics of the independent factors is not necessarily a weakness; by conducting many tests, it should eventually be possible to delimit for different groups of organisms the habitat and taxonomic conditions under which convergence is observed.

Finch communities

Despite potential shortcomings of the method, finch communities of different geographic regions were found to be convergent in similar habitats to a considerable degree. A substantial fraction of the worldwide variability in three of five community variables (number of species, mean size [PC1] and standard deviation in shape [PC2]) could be attributed to an effect of similar habitat type. Mean shape was also slightly convergent, and convergence of the fifth trait, standard deviation in size, was nearly significant. This pattern was observed even though no species were common to the same habitat type in different geographic regions (indeed, species were usually of different genera and fam-

TABLE 5. Convergence index (*C*) compared with effects of the historical or geographic region variable (*H*). Both *C* and *H* can vary between 0 and 1. Values of 1 indicate, respectively, complete convergence and complete dominance of historical/regional effects.

Community variable	Unweighted		Weighted	
	C	*H*	*C*	*H*
No. species	0.30*	0.13	. . .	. . .
Mean size	0.62**	0.02	0.61**	0.00
Mean shape	0.28*	0.40**	0.23	0.31**
SD of size	0.27	0.09	0.32	0.07
SD of shape	0.47*	0.08	0.48*	0.09

* $P < .05$, ** $P < .01$.

ilies), and different habitats in the same geographic region may have shared the same or closely related species. A significant effect of geographic region was also detected in one of the five community traits, mean shape.

Finch community similarity was not a reliable indicator of community convergence, although the two measures were partly related. Finch communities within the same habitat type were significantly similar for the most convergent variable, mean size. However, communities within the same habitat type were significantly different in mean shape, yet were also slightly convergent in this trait. Communities were neither significantly different nor similar for SD of shape, another strongly convergent trait.

Convergence as defined here indicates a predictive relationship between habitat type and the value of the community variable. In the finches, the precise causes of such relationships are as yet unknown. If other avian studies are a guide, then finch species diversity and morphological variation (SD of shape and possibly SD of size) may be associated with diversity of resources in habitats (e.g., Recher 1969, Roth 1976, Abbott et al. 1977, Schluter and Grant 1984*b*). Mean morphology (size and shape) of finches present might be associated with between-habitat variation in available food size or food position (Abbott et al. 1977, Schluter and Grant 1984*a, b*). For example, an effect of seed size on mean body size (PC1) is suggested in Fig. 3: mean finch size tends to be small in habitats dominated by grasses (e.g., tropical open grassland, tropical savanna woodland, and warm temperate grassland), and forest species are often relatively large. Field studies are necessary to determine whether such hypothesized associations are actually present.

The importance of interspecific interactions in determining convergence patterns would be more difficult to assess. Conceivably, convergence in most traits has resulted solely from individual convergence—species responding independently to resources. Convergence in species number would seem to require interactions at some point in the process of speciation and colonization, but alternative models have not been investigated.

However, results from similarity analyses suggest that interactions have been important, at least in one case. Significant similarity overall in mean size indicates a negative correlation in size between species within communities. This correlation in turn implies that body sizes of species within communities are more widely spaced than expected from a random assortment model. Possible interactions that might produce this pattern include competition between species of similar size, and mutualism between species of different size. The latter hypothesis is made somewhat plausible by experimental studies indicating indirect mutualistic effects of granivorous rodents on ants (Davidson et al. 1984) and possibly finches (D. B. Thompson, *personal communication*), although it is unclear whether different finch species could have such effects on each other.

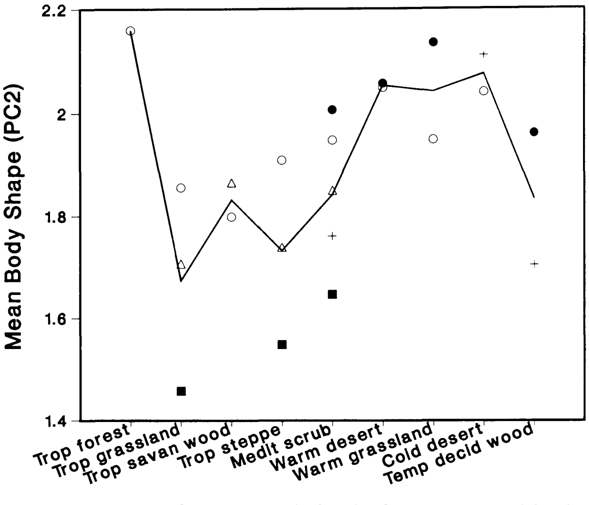

FIG. 4. Mean finch shape (PC2) in finch communities in relation to habitat type. Solid line connects average values of the different habitat types. Habitat types named in full in Table 1; symbols as in Fig. 2.

Finches of the different geographic regions have partly different origins and biogeographic histories. It is instructive, therefore, to contrast the effects of region with effects of habitat type on the individual community variables. The most interesting contrast is between (1) mean size, mainly an effect of habitat, and (2) mean shape, strongly affected by region. The reason for this difference is not clear, but it may be related to the generally greater ease with which size (PC1) responds to natural selection, a consequence of positive correlations between morphological characters (Boag 1983, Grant 1983, Price et al. 1984, Schluter 1984, D. Schluter and J. N. M. Smith, *personal observation*). Or, alternative morphological solutions to given habitat characteristics may exist for finch shape (PC2), and the one adopted is largely a matter of phylogenetic history. Third, it is possible that differences between regions result not from historical constraint, but from consistent differences between regions in characteristics of the resources available in habitats. This third hypothesis is testable with field studies; it would be rejected in favor of the first or second hypothesis, if finch species of identical size from different regions have the same feeding habits despite differences in shape. Such a result is made plausible by Fuentes' (1981) observation that mediterranean lizard communities are more convergent in habitat utilization than morphology.

Finally, since finches are only a component of a larger community of granivores, differences between communities in the same habitat type might be attributable in part to species not included in the analysis. No data are available to test this hypothesis, although Australia provides one suggestive example: low relative finch species diversity there is associated with a large radiation of parrots in similar habitats, many of which are similar in diet and body size to finches (e.g., Fry 1983). Similar procedures to those used for the finches could be used to investigate such patterns in greater detail for the larger communities of granivores.

ACKNOWLEDGMENTS

I'm indebted to various people for providing unpublished species lists and other information: G. W. Cox, J. W. Fitzpatrick, T. E. Lacher, G. H. Orians, T. Parker, R. B. Payne, J. V. Remsen, and F. Vuilleumier. I'm also grateful to the curatorial staffs at the Department of Ornithology, American Museum of Natural History, New York, and at the Museum of Vertebrate Zoology, University of California, Berkeley, for facilitating the use of their collections. F. Vuilleumier kindly sent me an early version of their report on mediterranean birds. D. R. Brooks, P. R. Grant, C. J. Krebs, P. Lavin, D. L. Pearson, T. D. Price, F. Vuilleumier, and a reviewer commented on the manuscript. J. Cooke and N. E. Heckman offered statistical advice. This work was supported in part by NSERC grant U0459. Computer funds were provided by the Institute of Animal Resource Ecology at the University of British Columbia.

LITERATURE CITED

Abbott, I., L. K. Abbott, and P. R. Grant. 1977. Comparative ecology of Galápagos ground finches (*Geospiza* Gould): evaluation of the importance of floristic diversity and interspecific competition. Ecological Monographs **47**:151–184.

Anderson, S. H. 1970. The avifaunal composition of Oregon white oak stands. Condor **72**:417–423.

Blondel, J., F. Vuilleumier, L. E. Marcus, and E. Terouanne. 1984. Is there ecomorphological convergence among mediterranean bird communities of Chile, California and France? Evolutionary Biology **18**:141–213.

Boag, P. T. 1983. The heritability of external morphology in Darwin's ground finches (*Geospiza*) on Isla Daphne Major, Galápagos. Evolution **37**:877–894.

Boag, P. T., and P. R. Grant. 1981. Intense natural selection in a population of Darwin's finches (Geospizinae) in the Galápagos. Science **214**:82–85.

Bourlière, F., editor. 1983. Tropical savannas. Elsevier, Amsterdam, The Netherlands.

Cody, M. L. 1974. Competition and the structure of bird communities. Princeton University Press, Princeton, New Jersey, USA.

Cody, M. L., and H. A. Mooney. 1978. Convergence versus nonconvergence in mediterranean-climate ecosystems. Annual Review of Ecology and Systematics **9**:265–321.

Davidson, D. W., R. S. Inouye, and J. H. Brown. 1984. Granivory in desert ecosystems: experimental evidence for indirect facilitation of ants by rodents. Ecology **65**:1780–1786.

Fisher, R. A. 1936. Has Mendel's work been rediscovered? Annals of Science **1**:115–137.

———. 1948. Statistical methods for research workers. 10th edition. Oliver and Boyd, Edinburgh, Scotland.

Fogden, M. P. L. 1972. The seasonality and population dynamics of equatorial forest birds in Sarawak. Ibis **114**: 307–343.

Fry, C. H. 1966. The ecological distribution of birds in northern Guinea savanna, Nigeria. Ostrich, Supplement **6**: 335–356.

———. 1970. The ecological distribution of birds in north-eastern Mato Grosso state, Brazil. Anais da Academia Brasileira de Ciências **42**:275–318.

———. 1980. An analysis of the avifauna of African northern tropical woodlands. Proceedings of the IVth Pan-African Ornithological Congress:77–88.

———. 1983. Birds in savanna ecosystems. Pages 337–357 *in* F. Bourlière, editor. Tropical savannas. Elsevier, Amsterdam, The Netherlands.

Fuentes, E. R. 1976. Ecological convergence of lizard communities in Chile and California. Ecology **57**:3–17.

———. 1981. Evolution of lizard niches in mediterranean habitats. Pages 417–444 *in* F. di Castri, D. W. Goodall, and R. L. Specht, editors. Mediterranean-type shrublands. Elsevier, Amsterdam, The Netherlands.

Goodwin, D. 1982. Estrildid finches of the world. Cornell University Press, Ithaca, New York, USA.

Grant, P. R. 1983. Inheritance of size and shape in a population of Darwin's finches, *Geospiza conirostris.* Proceedings of the Royal Society of London **B 220**:219–236.

Greig-Smith, P. W. 1976. The composition and habitat preferences of the avifauna of Mole National Park, Ghana. Bulletin of the Nigerian Ornithological Society **12**:49–66.

Hall, B. P., and R. E. Moreau. 1970. An atlas of speciation in African passerine birds. British Museum of Natural History, London, England.

Harrison, C. 1982. An atlas of the birds of the western palearctic. Princeton University Press, Princeton, New Jersey, USA.

Johnson, A. W. 1967. The birds of Chile and adjacent regions of Argentina, Bolivia, and Peru. Volume II. Platt Establecimientos Gráficos, Buenos Aires, Argentina.

Karr, J. R., and F. C. James. 1975. Eco-morphological configurations and convergent evolution in species and communities. Pages 258–291 *in* M. L. Cody and J. M. Diamond, editors. Ecology and evolution of communities. Belknap Press, Cambridge, Massachusetts, USA.

Lack, D. 1968. Tit niches in two worlds, or homage to G. E. Hutchinson. American Naturalist **103**:43–49.

Lack, D., and L. S. V. Venables. 1939. The habitat distribution of British woodland birds. Journal of Animal Ecology **8**:39–71.

Lawton, J. H. 1984. Non-competitive populations, non-convergent communities, and vacant niches: the herbivores of bracken. Pages 67–100 *in* D. R. Strong, Jr., D. Simberloff, L. G. Abele, and A. B. Thistle, editors. Ecological communities: conceptual issues and the evidence. Princeton University Press, Princeton, New Jersey, USA.

Logan, R. F. 1968. Causes, climates, and distributions of deserts. Pages 21–50 *in* G. W. Brown, Jr., editor. Volume I. Desert biology. Academic Press, New York, New York, USA.

Mares, M. A. 1976. Convergent evolution of desert rodents: multivariate analysis and zoogeographic implications. Paleobiology **2**:39–63.

McGinnies, W. G. 1979. Arid-land ecosystems—common features throughout the world. Pages 299–316 *in* D. W. Goodall and R. A. Perry, editors. Volume I. Arid-land ecosystems: structure, functioning and management. Cambridge University Press, Cambridge, England.

Meyer de Schauensee, R. 1966. The species of birds of South America and their distribution. Academy of Natural Sciences of Philadelphia, Pennsylvania, USA.

Moreau, R. E. 1935. A synecological study of Usambara, Tanganyika Territory, with particular reference to birds. Journal of Ecology **23**:1–43.

Morony, J. J., Jr., W. J. Bock, and J. Farrand, Jr. 1975. Reference list of the birds of the world. American Museum of Natural History, New York, New York, USA.

Narosky, T. 1978. Aves Argentinas (Field guide to the birds of Buenos Aires province). Department of Argentine Science Publications, Buenos Aires, Argentina.

Newton, I. 1973. Finches. Taplinger, New York, New York, USA.

Orians, G. H. 1969. The number of birds in some tropical forests. Ecology **50**:783–801.

Orians, G. H., and R. T. Paine. 1983. Convergent evolution at the community level. Pages 431–458 *in* D. J. Futuyma and M. Slatkin, editors. Coevolution. Sinauer, Sunderland, Massachusetts, USA.

Orians, G. H., and O. T. Solbrig, editors. 1977. Convergent evolution in warm deserts. Dowden, Hutchinson and Ross, Stroudsburg, Pennsylvania, USA.

Peterson, R., G. Mountford, and P. A. D. Hollom. 1983. A field guide to the birds of Britain and Europe. Fourth edition. Collins, London, England.

Pianka, E. R. 1973. The structure of lizard communities. Annual Review of Ecology and Systematics **4**:53–74.

Pianka, H. D., and E. R. Pianka. 1970. Bird censuses from desert localities in western Australia. Emu **70**:17–22.

Pimentel, R. A. 1979. Morphometrics. Kendall/Hunt, Dubuque, Iowa, USA.

Price, T. D., P. R. Grant, and P. T. Boag. 1984. Genetic changes in the morphological differentiation of Darwin's ground finches. Pages 49–66 *in* K. Wöhrmann and V. Loeschcke, editors. Population biology and evolution. Springer-Verlag, Berlin, Germany.

Pulliam, H. R., and M. R. Brand. 1975. The production and utilization of seeds in plains grasslands of southeastern Arizona. Ecology **56**:1158–1166.

Pulliam, H. R., and G. S. Mills. 1977. The use of space by wintering sparrows. Ecology **58**:1393–1399.

Rand, A. L., and E. T. Gilliard. 1968. Handbook of New Guinea birds. Natural History Press, Garden City, New York, USA.

Recher, H. F. 1969. Bird species diversity and habitat diversity in Australia and North America. American Naturalist **103**:75–80.

Ricklefs, R. E., and J. Travis. 1980. A morphological approach to the study of avian community organization. Auk **97**:321–338.

Roth, R. R. 1976. Spatial heterogeneity and bird species diversity. Ecology **76**:773–782.

Schluter, D. 1984. Morphological and phylogenetic relations among the Darwin's finches. Evolution **38**:921–930.

Schluter, D., and P. R. Grant. 1984*a*. Ecological correlates of morphological evolution in a Darwin's finch, *Geospiza difficilis.* Evolution **38**:856–869.

Schluter, D., and P. R. Grant. 1984*b*. Determinants of morphological patterns in communities of Darwin's finches. American Naturalist **123**:175–196.

Schluter, D., and J. N. M. Smith. 1986. Natural selection on beak and body size in the Song Sparrow. Evolution **40**: 221–231.

Schodde, R. 1981. Bird communities of the Australian mallee: composition, derivation, distribution, structure and seasonal cycles. Pages 387–415 *in* F. di Castri, D. W. Goodall, and R. L. Specht, editors. Mediterranean-type shrublands. Elsevier, Amsterdam, The Netherlands.

Schultz, B. 1983. On Levene's test and other statistics of variation. Evolutionary Theory **6**:197–203.

Snedecor, G. W., and W. G. Cochran. 1967. Statistical methods. Sixth edition. Iowa State University Press, Ames, Iowa, USA.

Sokal, R. R., and F. J. Rohlf. 1981. Biometry. Second edition. Freeman, New York, New York, USA.

Thomas, B. S. 1979. The birds of a ranch in the Venezuelan llanos. Pages 213–232 *in* J. F. Eisenberg, editor. Vertebrate ecology in the northern neotropics. Smithsonian Institution Press, Washington, D.C., USA.

Weathers, W. W. 1983. Birds of southern California's Deep Canyon. University of California Press, Berkeley, California, USA.

Winterbottom, J. M. 1966. Ecological distribution of birds in the indigenous vegetation of the South-west Cape. Ostrich **37**:76–91.

APPENDIX

Species lists and habitat types. Species names follow Morony et al. (1975).

Lowland Tropical Wet Forest

Costa Rica (Orians 1969)	Sarawak (Fogden 1972)
Pezopetes capitalis *Atlapetes brunneinucha* *Arremon aurantiirostris*	. . .

Lowland Tropical Open Grasslands

Brazilian campo, Mato Grosso (Fry 1970)	Fly River, S. New Guinea (Rand and Gilliard 1968)
Tiaris fuliginosa *Sporophila albogularis* *S. leucoptera* *Ammodramus humeralis* *Emberizoides herbicola*	*Neochmia phaeton* *Lonchura leucosticta* *L. nevermanni* *L. stygia*
Venezuelan llanos (Thomas 1979)	N. Ghana, Mole Park (Greig-Smith 1976)
Spiza americana *Sicalis flaveola* *Ammodramus humeralis*	*Euplectes afer* *E. hordeaceus* *E. orix* *E. melpoda* *Uraeginthus bengalus* *Lonchura cucullata*

Tropical Savanna Woodland

Brazilian cerrado, Mato Grosso (Fry 1970)	Guinea savanna, N. Ghana (Fry 1966, Greig-Smith 1976)
Saltator similis *Volatinia jacarina* *Sporophila plumbea* *S. caerulescens* *S. bouvreuil* *Oryzoborus angolensis* *Charitospiza eucosma* *Coryphospingus cucullatus* *C. pileatus* *Zonotrichia capensis*	*Emberiza tahapisi* *E. affinis* *Serinus gularis* *Ploceus luteolis* *Euplectes macrourus* *Plocepasser superciliosus* *Petronia dentata* *Vidua chalybeata* *V. orientalis* *Pytilia phoenicoptera* *Lagonosticta nigricollis* *L. rufopicta*

Tropical Thorn Steppe

Brazil caatinga (T. E. Lacher, *personal communication,* J. W. Fitzpatrick, *personal communication*)	Tanzania (Moreau 1935)
Passerina cyanea *Sporophila nigricollis* *S. lineola* *Sicalis flaveola* *Arremon taciturnus* *Volatinia jacarina* *Zonotrichia capensis* *Paraoria dominicana* *Coryphospingus pileatus*	*Uraeginthus bengalus* *U. ianthinogaster* *Ploceus velatus* *Serinus atrogularis* *S. donaldsoni* *Pytilia melba* *Estrilda charmosyna* *Vidua hypocherina*
	W. Australia (Pianka and Pianka 1970)
	Poephila guttata

APPENDIX

Continued.

Mediterranean Scrub	
California chaparral (Cody and Mooney 1978, Weathers 1983, D. Schluter, *personal observation*)	Chile matorral (Cody and Mooney 1978)
Pipilo erythrophthalmus *P. fuscus* *Carpodacus mexicanus* *Carduelis lawrencei* *Junco hyemalis* *Zonotrichia leucophrys* *Z. iliaca*	*Zonotrichia capensis* *Diuca diuca* *Carduelis barbata*
	Sardinia macchia (Cody and Mooney 1978)
	Fringilla coelebs *Carduelis carduelis* *C. chloris* *Serinus serinus*
South Africa Protea-fynbos (Winterbottom 1966, Cody and Mooney 1978)	
Serinus canicollis *S. sulphuratus* *Euplectes capensis* *Emberiza capensis*	
	Australia mallee (Schodde 1981)
	Poephila guttata *Emblema guttata*
Warm Temperate Desert	
Sonoran desert, California (Weathers 1983, D. Schluter, *personal observation*)	Monte desert, Argentina (G. H. Orians, *personal communication*)
Carpodacus mexicanus *Ammodramus sandwichensis* *Zonotrichia leucophrys* *Amphispiza belli* *A. bilineata* *Spizella breweri*	*Saltator aurantiirostris* *Zonotrichia capensis* *Poospiza melanoleuca* *P. ornata* *P. torquata* *Diuca diuca* *Saltatricula multicolor*
Warm Temperate Grassland	
Sonoita plains, Arizona (Pulliam and Brand 1975, Pulliam and Mills 1977)	Pampas, Buenos Aires (Narosky 1978)
Ammodramus savannarum *A. bairdii* *A. sandwichensis* *Pooecetes gramineus* *Calcarius ornatus*	*Zonotrichia capensis* *Sicalis flaveola* *S. luteola* *Ammodramus humeralis* *Sporophila ruficollis*
Cold Temperate Desert	
Patagonia, Santa Cruz (Meyer de Schauensee 1966, Johnson 1967)	Kazakhstan-Dzungarian desert (Harrison 1982)
Melanodera melanodera *Zonotrichia capensis* *Sicalis lebruni*	*Plectrophenax nivalis* *Calcarius lapponicus*
Temperate Deciduous Woodland	
Oak forest, Oregon (Anderson 1970)	Oak forest, England (Lack and Venables 1939)
Carpodacus mexicanus *Pipilo erythrophthalmus* *Junco hyemalis*	*Fringilla coelebs* *Pyrrhula pyrrhula*