WHY MOUNTAIN PASSES ARE HIGHER IN THE TROPICS*

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INTRODUCTION

This paper is designed to draw attention to the relation between tropical climatic uniformity at a given site and the effectiveness of topographic barriers adjacent to the site in preventing movements of plants and animals. This is not an attempt to explain tropical species diversity (see Pianka, 1966, for a review of this subject), but rather to discuss a factor that should be considered in any discussion of the relation between topographic and climatic diversity, and population isolation. Simpson (1964) states that "Small population ranges and numerous barriers against the spread and sympatry of related populations would therefore tend to increase density of species in a region as a whole. It will be suggested below that this is a factor in the increase of species densities in regions of high topographic relief. I do not, however, know of any evidence that it is more general or more effective in the tropics." I believe that the climatic regimes discussed below, and the reactions of organisms to them, indicate that topographic barriers may be more effective in the tropics. Mountain barriers and their temperature gradients in Central America, as contrasted to those in North America, are used as examples; but it is believed that the central idea equally applies to other tropical areas, types of barriers, and physical parameters.

There are three thoughts central to the argument to be developed: (1) in respect to temperature, it is the temperature gradient across a mountain range which determines its effectiveness as a barrier, rather than the absolute height; (2) in Central America, terrestrial temperature regimes are generally more uniform than North American ones, and differ in their patterns of overlap across geographic barriers; and (3) it can be assumed that animals and plants are evolutionarily adapted to, and/or have the ability to acclimate to, the temperatures normally encountered in their temporal and geographic habitat (or microhabitat).

MOUNTAIN TEMPERATURE GRADIENTS

Animals and plants encounter a mountain barrier as, among other things, different temperature regime from that to which they are acclimated or evolutionarily adapted. In general, and granting other environmental factors to be similar, this different temperature regime could occur as a band across a flat plain and still be just as impassable. The problem is the usual one of

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how much overlap there is between the temperature regime at the top of the pass and the valley below. This overlap bears two major considerations: (1) the number of hours, days, or months when the temperatures on the pass are similar to those in the valley, and (2) the amount of time and degree to which the organism can withstand temperatures different from those in the valley while it is crossing the pass. The outcomes of such crossings are theoretically measurable at all levels, from the single individual which establishes a new population but is never joined by further immigrating members, to varying rates of individual organism flow (sometimes resulting in gene flow); there will be some level where the overlap is so great that for a given population the barrier no longer exists. However, for some other population with less ability to withstand previously unexperienced temperatures, the same region may be an absolute barrier.

CLIMATIC UNIFORMITY AND OVERLAP

There are areas of great temperature stability in temperate North America (e.g., coastal bays backed by low mountain ranges such as the area of San Francisco Bay, California), and areas of large temperature fluctuation in Central America (e.g., areas of well marked dry and wet seasons, and under the influence of cold air masses off the Caribbean during the northern winter, e.g., Veracruz, Mexico). However, contrast of weather records from a Central American country with those of any state in the United States will quickly show that, in general, the Central American temperature regime at a given site is more uniform on a monthly and daily basis at any altitude of distance from the seas than that of a geographically comparable site in the United States (Fig. 1; representative monthly means of the daily means, maxima and minima, for six sites in Costa Rica and in the United States). It is clear from Fig. 1 that from site to site there may be large differences in monthly temperatures; but at a given site, relative uniformity is the rule in a representative tropical country such as Costa Rica.

In respect to the impassability of mountain barriers, and intimately related to the relative uniformity of temperature regimes, the amount of overlap between the weather regime at the top of the pass and the valley below is of utmost importance; the more overlap, the less of a temperature barrier the mountain presents, and the greater the difference between monthly mean maxima and minima in the two adjacent regimes, the more overlap there is likely to be. Six representative overlap patterns in the United States and Costa Rica are exemplified in Fig. 1. For Costa Rica, the weather records were extracted from the Annuario Meteorologico for 1961 and 1964. For the United States, they were taken from U.S. Department of Commerce Weather Bureau reports (1959) and Marr (1961). Both sets were chosen on the basis of availability of maxima and minima weather data, and their position on altitudinal transects. In Fig. 1, patterns of overlap are presented from virtually no overlap (a: Costa Rica—Palmar Sur to Villa Mills, 16 to 3096 meters; d: Colorado—Grand Junction to the top of the front range behind Boulder, 1616 to 4100 meters), to high containment of the mountaintop regime within that of the valley below (c: Costa Rica—Palmar Sur to San Isidro del General, 16 to 703 meters; f: California—Fresno to Bishop, 110 to 1369 meters).

The form of the Costa Rican temperature regimes and their overlaps in Fig. 1 is clearly not the same as that of the United States' regimes. The following traits of these representative patterns are of importance to organisms living in one regime and confronted with the problem of moving through the other temperature regime to get to another area, or merely into the other regime for short-term activities.

1. The temperate regimes involve much greater changes over the year than the tropical, in respect to monthly values, and daily values (not shown in the figures, but clear from weather records).

2. The variation in difference between the monthly mean maxima and minima, across the change of seasons, is greater in the temperate examples than the tropical ones.

3. The time of maximum difference between the monthly mean maxima and minima is the summer (growing season) in the temperate examples and is the dry season (dormancy season) in the tropical examples.

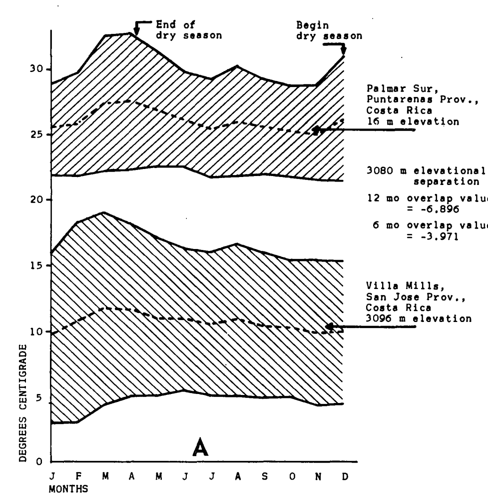
4. The absolute differences between monthly mean maxima and minima are greater in the temperate examples during the summer than in the tropical examples during the rainy season.

5. The greatest amount of overlap between temperature regimes occurs during the growing season in the temperate examples but during the dry season in the tropical examples.

It is hypothesized that the amount of overlap between two temperature adjacent regimes should be greater in the temperate region than in the tropics, for any given elevational difference between the sites of the two adjacent regimes, because of the greater distances between the extremes for the temperate regimes as contrasted to tropical. To test this, overlap values between the temperature regimes of 15 pairs of sites in Costa Rica and 15 pairs of sites in the continental United States (Appendix) were calculated by the following formula:

$$\text{overlap value} = \sum_{i=1}^{12} \frac{d_i}{\sqrt{R_{1i}R_{2i}}}$$

where d_i is the amount (in degrees) of one regime that is included within the other, for the ith month. If one regime is not included within the other, d_i is considered negative and has the value of the number of degrees separating the regimes. R_{1i} is the difference in degrees between the monthly mean maximum and minimum for the ith month of the higher elevational regime and R_{2i} is the equivalent value for the lower elevational regime. Overlap is being considered in units of the geometric mean between R_{1i} and R_{2i}; hence it is the *relative* overlap, called hereafter simply "overlap." The overlap value has the property that if the monthly mean maxima of the higher elevation regime are equal to the monthly mean minima of the lower elevation regime for all 12 months, the overlap value is zero (a case intermediate



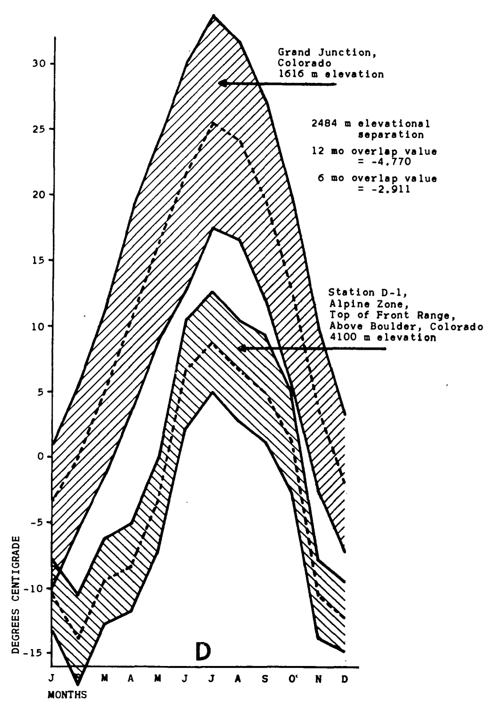
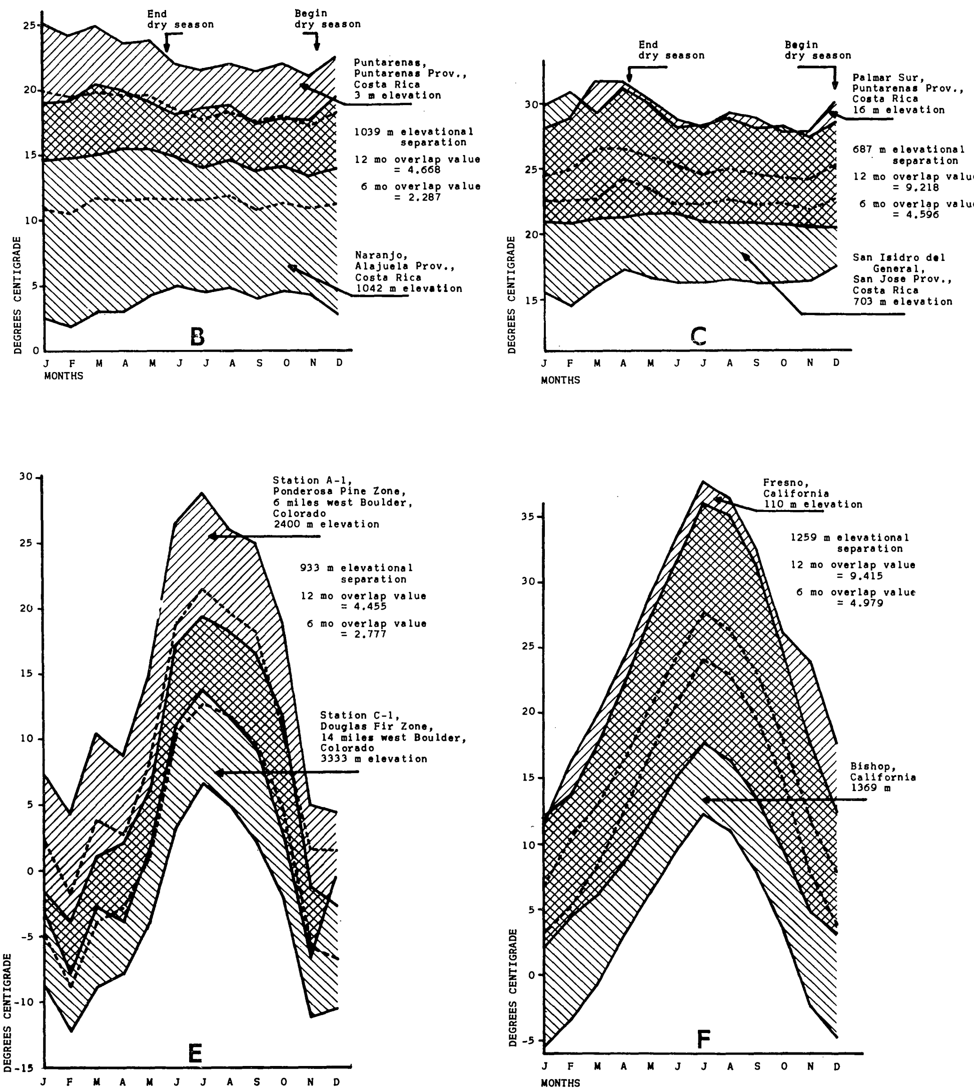


FIG. 1. Representative temperature regimes of three tropical (A, B, C) sites and three temperate (D, E, F) sites. Each graph figures two regimes. The dotted lines trace the monthly temperature means; in all cases the mean of the lower elevation regime is above that of the higher elevation mean. Solid lines trace the monthly means of daily maxima and minima; in all cases the two lower solid lines in each



graph represent the monthly mean minima of the two regimes, with the lowermost representing the higher elevation site. Overlap between temperature regimes of adjacent sites is portrayed by cross-hatching, and increases from A and D to C and F. All graphs are to the same scale.

between that exemplified in Fig. 1a and 1b). As overlap increases, the overlap value increases to a value of 12 at the point where the two temperature regimes are congruent. Complete inclusion of one regime in the other does not guarantee maximal overlap (e.g., Fig. 1c, 1f). There is no lower limit to negative overlap values (e.g., Fig. 1a, 1d) as elevational separation between two regimes become progressively greater.

It is clear that the amount of overlap between the temperature regime of the valley bottom and the temperature regime on the mountainside above, at a specific geographic area, is primarily a function of the distance in elevation between the two weather stations. Thus the overlap between a pair of adjacent regimes in the tropics can only be compared with a temperate example of overlap where the elevational separation is similar in the two geographic areas. In Fig. 2 and 3, overlap values for each of the 30 pairs of adjacent regimes in Appendix A are plotted against the amount of elevational difference between the regimes of each pair. In Fig. 2, the overlap values are calculated for the entire 12 months of the year, while in Fig. 3, they are calculated for the six months of the growing season in the temperate examples (April through September) and for the first six months of the rainy season in the Costa Rican examples (May through October). Ideally, all 30 elevational transects should have been chosen from areas of similar rainfall patterns, but these weather data are not available.

From examination of these scattergrams and their regression lines, a number of statements have been generated that have a bearing on the effectiveness of temperature barriers in restricting the movements of organisms.

1. The overlap values of all 30 pairs of regimes for both 12 and 6 month periods, show an apparently linear relation of decreasing overlap with increasing elevational separation between the lowland and highland temperature regimes. It is this relation that leads to the classical feeling that effectiveness of mountain barriers is roughly related to their height.

2. The 12 month regression line (line I) for the Costa Rican sites has the steepest slope of the three lines in Fig. 2, but is not significantly different in slope from the 12 month regression line (line II) for all the United States' sites (line I, $b = -149$; line II, $b = -114$, $t_{26\,\mathrm{d.f.}} = 1.084$). However, the t value is high enough to suspect a relation that is obscured by the small sample size and high variance. If line I and line II are really representative of two different populations, as they appear to be following the manipulation described under 3 below, then it can be said that the overlap values demonstrated across the tropical elevational separations are less than those of the temperate examples, and become proportionally less as the elevational separation becomes less.

3. When the regression lines for the six months values are compared (Fig. 3) their slopes are highly significantly different (line IV, $b = -299$; line V, $b = -208$; $t_{26\,\mathrm{d.f.}} = 3.1531$) indicating that there are two separate populations of overlap values. This indicates that there is more dissimilarity between the overlaps of the Costa Rican paired regimes and the overlaps of the United States' paired regimes during the growing season than during the dormancy

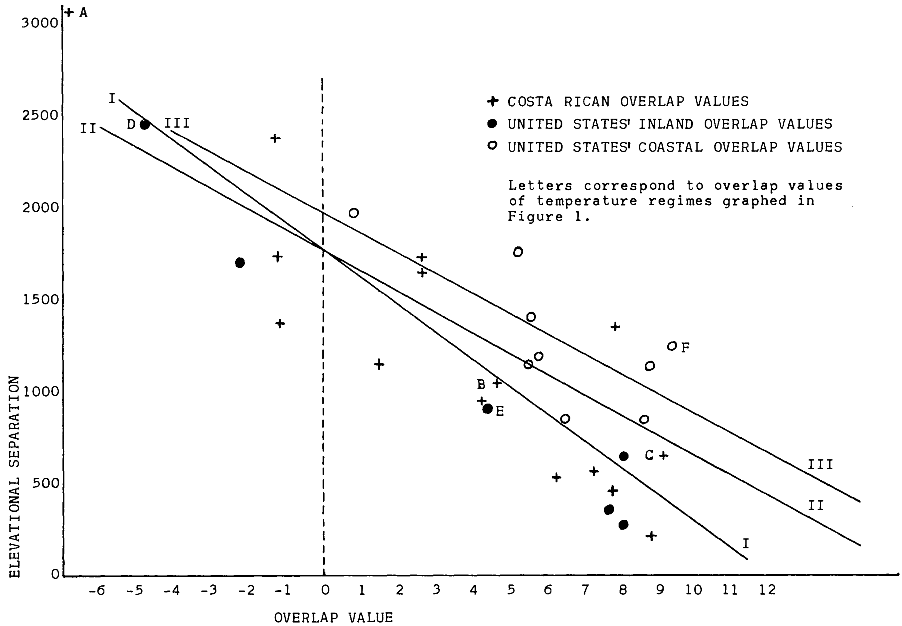


FIG. 2. Regression of overlap values for a 12-month period on elevational separation between the pair of temperature regimes for which the overlap value was calculated. Line I is that for 15 Costa Rican sites, line II is that for 15 United States' sites, and line III is that for the nine coastal sites included within the sites for line II.

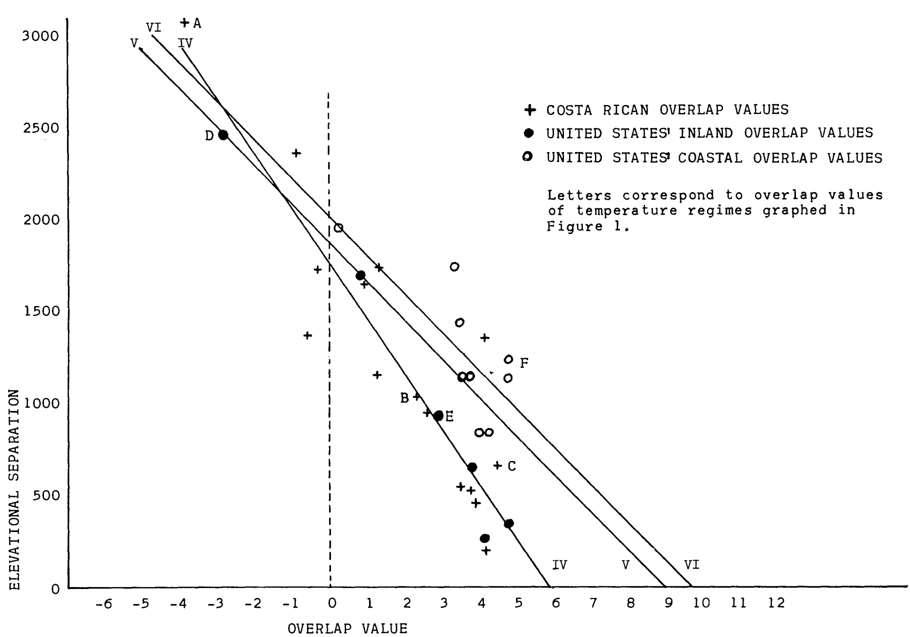


FIG. 3. The overlap values calculated for the six summer months for the temperate regimes (April through September) and the first six months of the rainy season for the tropical regimes (May through November). Line IV, Costa Rican sites; V, all United States sites; VI, nine U. S. coastal sites.

season. However, it should be noted that the removal of the winter months from the temperate data removes in absolute value much more of the variation in overlap from month to month than does the removal of the dry season months from the Costa Rican data.

4. If the six continental United States' records are removed, to make the relation to oceans more equivalent between the United States and Costa Rican sites, the 12 month regression line (line II) moves up the overlap scale to become line III (overlap value changes from 5.22 to 6.31), but lines II and III remain parallel (line II, $b = -114$; line III, $b = -110$; $t_{20\,\mathrm{d.f.}} = 0.1948$). The six-month regression line also moves following this manipulation but to a lesser extent (mean overlap changes from 3.335 to 3.650). From the distribution of the midcontinental United States' points in Fig. 2 and 3, it can be seen that, in respect to overlap for a given elevational separation, the Costa Rican sites have more in common with the midcontinental United States' sites than with the coastal ones. In other words, maximal differences between tropical and temperate overlaps are recorded when coastal areas of the United States are compared with Costa Rican transects. It should be emphasized at this point that virtually all of the Costa Rican records are coastal in the sense that no point in the country is more than about 125 miles from an ocean. In retrospect, it would seem advisable to remove this major source of variation in later comparisons of this type.

5. The variation of overlap value is great for any given elevational separation, and a given overlap value may be representative of a wide range of elevational separations in both the Costa Rican and United States data. In Fig. 3, based on six-month values, the variation in overlap for a given elevational separation is reduced. To compare any two barriers involving an elevational separation, it is clear from this that the actual amount of overlap between the upper and lower temperature regimes should be determined, since the same elevational separation on two different mountain ranges can yield quite different overlap values.

6. There is no obvious trend in change of amount of variation in overlap value along the various regression lines. For example, at an elevational separation of approximately 1700 m, the overlap values range from -2.25 to 5.40, and at 1150 m, they range from 1.50 to 8.75 (Fig. 2). This, coupled with the apparent linearity of the data, indicates that at one latitude the overlaps between temperature regimes lying at sea level and 500 m elevation should have about the same mean values and the same variances as overlaps between temperature regimes at 500 m and at 1000 m.

7. There is a point where the Costa Rican and United States' regression lines intersect (Fig. 2, zero overlap, 1780 m elevational separation; Fig. 3, -1.2 overlap, 2100 m elevational separation), and, thus, for these elevational separations, the overlap for the paired regimes are the same in the tropical and temperate example. It is notable that this point of overlap equality is at a larger elevational separation when the six-month records are considered. This indicates that the Costa Rican and United States' overlap values are even more dissimilar during the growing seasons.

8. The temperate and tropical regression lines become increasingly divergent as the elevational separation becomes less; the smaller the elevational separation, the greater will be the difference between a temperate and a tropical overlap value calculated for a pair of adjacent temperature regimes. It is not possible to compare the regression lines (I and II, IV and V) on the basis of population means since the slopes of the lines are not similar. However, in both Fig. 2 and 3, the temperate regression lines are above the Costa Rican lines, indicating that the more "tropical" the physical environment pattern, the more important are the smaller topographic features.

While there is great variation around the regression lines in Fig. 2 and 3, a major part of this variation could be removed if many weather records were available for a specific set of slopes of a major mountain range in Costa Rica, and another in the United States, both with similar exposures to an ocean and similar precipitation regimes. This statement is based on the observation that in the few cases where a long elevational transect could be broken up into component temperature regimes and an overlap value calculated between each pair of regimes, the points yield a straight line with almost no deviation from the line (e.g., Costa Rica: the overlaps of Puntarenas-Esparta, Puntarenas-Naranjo, Puntarenas-San Jose, Esparta-San Jose, and Naranjo-San Jose form a very straight line). A second source of variation, implied in the preceding paragraph, is that the points from different precipitation regimes tend to form different lines; but within a given regime, the points form very straight lines.

The minimum of the valley and the maximum on the pass do not occur at the same time during the 24 hour cycle. Thus it is that at any one point in time there is probably little or no overlap between two temperature regimes separated by more than 500 m. However, an organism is present for long periods of time and thus is subjected to all the temperature levels in its habitat. Thus the overlap as graphed in Fig. 1 and quantified in Fig. 2 and 3 is a measure of the amount of similarity between the temperature regimes experienced by an organism living in the valley bottom and then moving up and over the pass. If all the overlap patterns had the same shape as those of Costa Rica, the tropical and temperate values could be compared without qualification (as in Fig. 2). However, the manipulation used in Fig. 3 is in part justified by the fact that major periods of animal and plant activity are during the northern summer and tropical rainy season, and a purpose of this paper is to illustrate the relation between overlap and activities of organisms.

ACCLIMATION AND EVOLUTIONARY ADAPTATION

Throughout this discussion it is assumed that an organism is less likely to evolve mechanisms to survive at a given temperature if that temperature falls outside of the temperature regime of the organism's habitat than if it falls within it.

Allee et al. (1949, p. 538-539) in summarizing Payne's studies of cold hardiness in insects, has stated this in the following manner: "(1) degree of cold hardiness was [positively] correlated with seasonal periodicity of temperature, and (2) that degree of cold hardiness in a series of species, from a variety of habitats in terrestrial communities, was [positively] correlated with the normal seasonal fluctuation of temperature in that community or habitat in which a particular species was normally resident.'' In other words, the larger the usual variation around the mean environmental values, the higher the probability that an organism will survive a given deviation from that mean; this should apply to daily, as well as seasonal, predictability of deviations. This relation has been indicated in another manner by DuRant and Fox (1966) when discussing the effect of soil moisture on soil arthropods. Those in soil of consistently lower moisture content were more sensitive to small changes in soil moisture content than those in soils of consistently higher moisture content; i.e., the reaction of an organism to a change in the environment is dependent upon the relative as well as absolute values of that change.

It is reasonable to expect that an organism living within the relatively uniform tropical temperature regimes depicted in Fig. 1 (a, b, c) will more probably be acclimated and evolutionarily adapted to a narrower absolute range of temperatures than one which lives within the more highly fluctuating temperature ranges depicted in Fig. 1 (d, e, f). ''Fluctuation'' as used above applies to the variation in the monthly means across the 12-month period, the changes in the difference between the monthly means of the daily maxima and minima, and the variation in maxima and minima from day to day. This should be true even if the organism is in a resting stage during some part of the year and thus, by regulating its activity, it places itself in a more uniform environment during major activity periods. It seems likely that there will be residual ability to withstand temperatures outside of the usual habitat values at the times of activity, as physiological ''by-products'' of the mechanisms that allow survival during the times of inactivity.

The relation between relative uniformity of the normal habitat and the dispersal ability of the organism is well shown with weed or fugitive species of both plants and animals. These organisms customarily live in disturbed sites and have many mechanisms for survival under the physical extremes present at these places. While they have evolved great dispersal ability as a necessary part of the strategy of living in the temporary habitat of disturbed sites, mechanisms for living in this variable habitat are of obvious value in crossing the various temperature, etc., regimes necessary to find further disturbed sites.

Assuming the same amount of overlap between the temperature regimes of a valley bottom, and the pass above, at a tropical and at a temperate site with equal elevational separation, it is proposed that a tropical organism from the valley bottom is less likely to get over the pass than is a temperate organism, because the tropical organism has a higher probability of encountering temperatures to which it is neither acclimated nor evolutionarily adapted than does the temperate organism. In addition to the monthly changes exemplified in Fig. 1, this is due to the central fact that in the Costa Rican temperature regimes, for example, if the monthly mean maxima and minima are 28 and 19 C, respectively, the standard deviation of each of these means is normally less than 2 C, while the standard deviation of a similar pair of values for the United States' records in Fig. 2 and 3 would be 4 to 5 C.

However, as has been shown with the six-months values (Fig. 3) and indicated with the 12-month values (Fig. 2) for a given elevational difference in Costa Rica and in the United States, there is likely to be more overlap between the temperate adjacent temperature regimes than the tropical ones. In this case, the tropical organism has even less chance than the temperate one of getting over a pass.

This is why it is postulated that mountains are higher in the tropics figuratively speaking; they are harder to get over because, for a given elevational separation, the probability is lower in the tropics that a given temperature found at the higher elevation will fall within the temperature regime of the lower elevation than is the case in the temperate area. For example, an insect living in the forest around Puerto Viejo, Costa Rica (83 m elev.) is subjected to an annual absolute range of about 37 to 17 C; if the insect lives anywhere other than the upper surface of the canopy, the range is reduced by the insulating value of the vegetation. To move up to and over the adjacent pass at Vara Blanca, Costa Rica (1804 m elev.) it must pass through an area that is rarely, if ever, over 22 C but ranges down to 8 C (a similar regime is depicted in Fig. 1b). An insect living around Sacramento, California (8 m elev.) is subjected to an annual range of at least 46 to −9 C. To cross the Sierra Nevada at Blue Canyon, California (1760 m elev.), it must pass through an area that experiences annual ranges of about 31 to 8 C (a similar regime is depicted in Fig. 1e). The 12-month overlap value calculated for the Puerto Viejo–Vara Blanca transect is 2.648 and that for the Sacramento–Blue Canyon transect is 5.358. During the summer months, the temperature regime at Blue Canyon is almost completely contained within that of Sacramento. Thus the temperate elevational separation of 1758 m should not be nearly as inimical to animal movements as the tropical elevational spread of 1721 m.

DISCUSSION

The relation between the climatic uniformity of a habitat and the ability of the organisms living in that habitat to cross adjacent areas with different climatic regimes may indicate a general concept. In respect to temperature, valleys may figuratively be deeper to an organism living on the ridge top in the tropics than in a temperate area. In respect to rainfall patterns, one would expect the following situation. An organism living in an area with a uniform water supply (ground water or rainfall) should have more difficulty in crossing an adjacent desert than would an organism living in an area with a six-month dry season. Seasonal swamp inhabitants should be able to cross rivers more readily than those organisms which always live on the dry ground around the swamp. In other words, the greater the fluctuation of the environment in the habitat of the organism, the higher the probability that it will not encounter an unbearable combination of events in the adjacent different habitat that it is attempting to cross. Since the tropics are in general more uniform in relation to temperature, and often in respect to rainfall patterns, for a given habitat or site, it is expected that barriers involving gradients in temperature or rainfall are more effective in preventing dispersal in the tropics.

It is clear that the "tropics" are not a single phenomenon. Classical tropical climates and vegetation are at the intersections of the high ends of gradients of uniform solar energy and capture rainfall patterns. The classical tropical image is destroyed as one moves into seasonality in rainfall pattern and temperature, upward into colder elevations, laterally into areas of uniform dryness, or into areas of increased unpredictability in the absolute values and pattern of the physical environment. Thus it is that overlaps between temperature regimes in the tropics and temperate zones cannot be precisely compared, and the effect of rainfall patterns on temperature regimes is associated with much of the variation seen in Fig. 2 and 3.

Even if the "significant differences" in overlap values in Costa Rica and the United States are not truly representative of tropical and temperate temperature regime overlaps, the amount of overlap between a temperature regime at the pass and the temperature regime in the valley below are characteristcis of valley-mountain systems that should be considered in discussions of mountains as barriers between populations. Secondly, there is so much variation in the overlap value for a given elevational separation along both temperate and tropical transects that each pair of transects should be regarded as a special case in specific studies of barriers.

Since overlap values are not the same throughout the year over a specific elevational separation at a specific site, the evolutionary timing of the dispersal phases of organisms that use immigration across barriers as a strategy may be associated with the periods of greatest overlap. On the other hand, if segregation of populations is of selective value, as may well be the case if the dispersal forms are also the sexual forms, timing of production of dispersal forms may "move" away from the time of greatest overlap through evolutionary selection. In other words, if it is detrimental to the population to mate with other sexuals "coming over the mountain," then this can be avoided by production of sexuals at a time when other sexuals are not coming over the mountain (group selection is not being invoked here).

It is not intended that the idea of greater effectiveness of tropical barriers as compared with temperate ones of equal absolute magnitude be offered as an explanation of tropical species diversity. However, it is my intent to emphasize the concept that greater sensitivity to change is promoted by less frequent contact with that change.

With a few notable exceptions (e.g., Schulz' 1960 analysis of dry seasons in Suriname), investigators in tropical areas have generally ignored the problem that the usefulness of a given unit of scale in portraying constancy, variation, and variance, is directly related to the organism's sensitivity to the part of the environment being measured; while we are intuitively satisfied with monthly values in understanding the four temperate seasons, it is clear that monthly values are hardly adequate in a tropical area such as Costa Rica where eight seasons are customarily recognized (from the beginning of the rainy season: invierno, veranielo, canicula, invierno, temporales, chubascos, verano fresco, and verano caliente). That eight seasons are recognized in a supposedly more uniform climate underscores the topic of this paper. While the seasonal and daily variations in Costa Rica are smaller than those of most areas in the United States, they are simultaneously much more predictable; thus, the behavioral and developmental patterns of populations are more easily, in an evolutionary sense, associated with them than they are with unpredictable changes of equal magnitude. However, it is to be expected that more precise fitting of population activities to more predictable environmental conditions should lead to less ability to tolerate the different conditions encountered outside of the usual temporal and spatial habitat. This leads directly to the idea that the more predictable the environment, the smaller the change in that environment needs to be to serve as an immediate or long-term barrier to dispersal. This should be important in understanding the higher fidelity of tropical animals and plants to spatial and to temporal habitats which are set off by apparently minor differences in physical conditions (as compared with temperate habitats). This fidelity is experienced by anyone collecting in tropical areas, and has been documented (e.g., MacArthur, Recher, and Cody [1966] and included references, Janzen and Schoener [1967]). Such fidelity is obviously an important element of the structure of communities; and it is proposed that the increase in predictability of the physical and biotic environment, as one progresses from classical temperate environmental regimes to tropical ones, is causally related in a positive manner to the increase in species' fidelity to their habitats across the same progression. Further, this is a mutually reinforcing system whereby increased biotic fidelity leads to further biotic fidelity through the medium of interdependency of members of the same food chain.

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LITERATURE CITED

Allee, W. C., A. E Emerson, O. Park, T. Park, and K. P. Schmidt. 1949. Principles of animal ecology. Saunders Co., Philadelphia. 837 p.

Annuario Meteorologico. 1961. Servicio Meteorologico Nacional, Seccion Climatologia. San Jose, Costa Rica. 43 p.

______. 1964. Servicio Meteorologico Nacional, Seccion Climatologia. San Jose, Costa Rica. 61 p.

DuRant, J. A., and R. C. Fox. 1966. Some arthropods of the forest floor in pine and hardwood forests in the South Carolina Piedmont region. Ann. Entomol. Soc. Amer. 59:202-207.

Janzen, D. H., and T. W. Schoener. 1967. Differences in insect abundance and diversity between wetter and drier sites during a tropical dry season. Ecology (in press).

MacArthur, R. H., H. Recher, and M. Cody. 1966. On the relation between habitat selection and species diversity. Amer. Natur. 100:319-332.

Marr, J. W. 1961. Ecosystems of the east slope of the Front Range in Colorado. University of Colorado Studies, Series in Biology No. 8, Univ. Colorado Press. 134 p.

Pianka, E. R. 1966. Latitudinal gradients in species diversity: a review of concepts. Amer. Natur. 100:33-46.

Schulz, J. P. 1960. Ecological studies on rain forest in northern Suriname. Verhandelingen der Koniklijke Nederlandse Akademie van Wetenschappen, Afd. Natuurkunde 53(1):1-267.

Simpson, G. G. 1964. Species density of North American recent mammals. Syst. Zool. 13:57-73.

U.S. Department of Commerce Weather Bureau. 1959. Climates of the States; Colorado (1959), California (1959), Oregon (1960), New Hampshire (1959), Idaho (1959), Nevada (1960). U. S. Government Printing Office.

APPENDIX

Localities of pairs of temperature regimes from which overlap values were calculated

Locality	Elevation of site (m)	Degrees N Latitude	Elevational separation	12 month overlap value	6 month overlap value
United States:					
(1) Sacramento, California	8	38° 35'	1173 m	5.712	3.774
Mount Shasta, California	1181	41° 19'			
(2) Los Angeles, California	100	34° 03'	1406 m	5.462	3.547
Sandburg, California	1506	34° 45'			
(3) Eureka, California	14	40° 48'	1167 m	5.616	3.528
Mount Shasta, California	1181	41° 19'			
(4) Roseburg, Oregon	168	43° 14'	1107 m	8.862	4.806
Sexton Summit, Oregon	1275	42° 37'			
(5) Fresno, California	110	36° 46'	1259 m	9.415	4.979
Bishop, California	1369	37° 22'			
(6) Sacramento, California	8	38° 35'	1752 m	5.358	3.460
Blue Canyon, California	1760	39° 17'			
(7) Pendleton, Oregon	497	45° 41'	853 m	6.662	4.300
Meacham, Oregon	1350	45° 30'			
(8) Concord, New Hampshire	113	43° 12'	1974 m	0.982	0.238
Mount Washington Observatory, New Hampshire	2087	44° 16'			
(9) Medford, Oregon	437	42° 22'	838 m	8.735	4.215
Sexton Summit, Oregon	1275	42° 37'			
(10) Las Vegas, Nevada	721	36° 05'	648 m	8.038	3.703
Bishop, California	1369	37° 22'			
(11) Reno, Nevada	1466	39° 30'	294 m	8.308	4.123
Blue Canyon, California	1760	39° 17'			
(12) Boise, Idaho	944	43° 34'	367 m	7.771	4.818
Idaho Falls, Idaho	1311	43° 32'			

APPENDIX (*Continued*)

Locality	Elevation of site (m)	Degrees N Latitude	Elevational separation	12 month overlap value	6 month overlap value
(13) Station A-1, Ponderosa Pine Zone, 6 miles west of Boulder, Colorado	2400	40°	1700 m	−2.291	−0.935
Alpine Zone, Top of Front Range above Boulder, Colorado	4100	40°			
(14) Grand Junction, Colorado	1616	39° 07'	2484 m	−4.770	−2.469
Station D-1, Alpine Zone, Top of Front Range above Boulder, Colorado	4100	40°			
(15) Station A-1, Ponderosa Pine Zone, 6 miles west of Boulder, Colorado	2400	40°	933 m	4.453	2.777
Station C-1, Douglas Fir Zone, 14 miles west of Boulder, Colorado	3333	40°			
Costa Rica:					
(16) Cairo, Limon Prov.	94	10° 07'	1341 m	7.717	4.027
Cartago, Cartago Prov.	1435	9° 40'			
(17) Palmar Sur, Puntarenas Prov.	16	8° 57'	3080 m	−6.896	−3.971
Villa Mills, Puntarenas Prov.	3096	9° 34'			
(18) Puntarenas, Puntarenas Prov.	3	9° 58'	205 m	8.779	4.192
Esparta, Puntarenas Prov.	208	9° 59'			
(19) Palmar Sur, Puntarenas Prov.	16	8° 57'	687 m	9.218	4.596
San Isidro del General, San Jose Prov.	703	9° 22'			
(20) Cartago, Cartago Prov.	1435	9° 40'	1661 m	2.656	0.969
Villa Mills, San Jose Prov.	3096	9° 34'			
(21) Esparta, Puntarenas Prov.	208	9° 59'	964 m	4.292	2.655
San Jose, San Jose Prov.	1172	9° 56'			
(22) Puerto Viejo, Heredia Prov.	89	10° 26'	1715 m	2.648	1.090
Vara Blanca, Heredia Prov.	1814	10° 10'			
(23) Canas, Guanacaste Prov.	45	10° 25'	517 m	6.291	3.689
Tilaran, Guanacaste Prov.	562	10° 28'			

APPENDIX (*Continued*)

(24) Quebrada Azul, Alajuela Prov. Tilaran, Guanacaste Prov.	83 562	10° 24' 10° 28'	479 m	7.895	3.900
(25) Quebrada Azul, Alajuela Prov. Villa Quesada, Alajuela Prov.	83 656	10° 24' 10° 17'	567 m	7.366	3.511
(26) Puntarenas, Puntarenas Prov. Naranjo, Alajuela Prov.	3 1042	9° 58' 10° 06'	1039 m	4.668	2.287
(27) Quebrada Azul, Alajuela Prov. Vara Blanca, Heredia Prov.	83 1814	10° 24' 10° 10'	1731 m	−1.016	−0.351
(28) Puntarenas, Puntarenas Prov. San Jose, San Jose Prov.	3 1172	9° 58' 9° 56'	1169 m	1.513	1.179
(29) Puntarenas, Puntarenas Prov. Monteverde, Puntarenas Prov.	3 1380	9° 58' 10° 20'	1377 m	−1.147	−0.590
(30) San Isidro del General, San Jose Prov. Villa Mills, San Jose Prov.	703 3096	9° 22' 9° 34'	2393 m	−1.162	−0.987