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# Species-energy theory: an extension of species-area theory

**David Hamilton Wright**

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A more general biogeographic theory of island species number is produced by replacing area with a more direct measure of available energy in the models of MacArthur and Wilson and Preston. This theory, species-energy theory, extends beyond species-area theory in that it applies to islands that differ in their per-unit-area productivity due to differences in physical environment, such as climate. Examination of data on species number of angiosperms and of land and freshwater birds on islands worldwide, ranging from Greenland and Spitsbergen to New Guinea and Jamaica, demonstrates that species-energy theory can explain 70 to 80% of the variation in species number on such widely varying islands, and further suggests the existence of regular geographic trends in resource utilization or species-abundance patterns. The concepts embodied in species-energy theory can in principle be used to develop predictions of species' abundances and probabilities of occurrence on an island. Species-energy theory may also provide a unified basis for understanding a broad set of observations of patterns in species diversity.

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Более общая биогеографическая теория числа островных видов создана путем репликации территории, где проводились прямые измерения использования энергии к моделям Мак Артура и Уилсона и Пристона. Эта теория, теория энергетики видов, выходит за рамки теории ареала вида, в которой она использовалась для островов, различающихся по продуктивности на единицу площади в результате различий таких физических факторов, как климат. Анализ данных по числу видов покрытосемянных растений и наземных и пресноводных видов птиц на островах всего мира от Гренландии и Шпицбергена до Новой Гвинеи и Ямайки показал, что теория энергетики видов может объяснить 70–80% вариаций в числе видов на таких сильно различающихся отсровах и подтверждает наличие закономерных географических тенденций в характере утилизации ресурсов или видовом разнообразии. Концепции, включенные в теорию энергетики видов, могут в принципе использоваться для предсказания видового обилия и вероятности встречаемости на острове. Теория энергетики видов может также представить общую основу для понимания широкого круга исследований типов видового разнообразия.

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## Introduction

Ecologists have long pondered how to predict how many species will occur in a community. Recent work (DeAngelis 1980, Brown 1981, Yodzis 1981) suggests, in agreement with earlier authors (Hutchinson 1959, Connell and Orias 1964, MacArthur 1965, 1972: 183) that the energy supply supporting a community limits the capacity of that community to contain species. This paper considers the relevance of a broad set of observations relating energy supply and species diversity and abundance, and attempts to provide a unified basis for understanding these patterns. To do this, I modify two important ecological models of species number and show how energy supply can limit species number. The modified theory has additional explanatory power and also raises new questions.

One of the most productive ecological models which addresses patterns of species number has been the equilibrium theory of island biogeography, proposed by MacArthur and Wilson (1963, 1967), which portrays the regulation of species diversity as a dynamic process where immigration opposes extinction. The primary factors affecting insular immigration and extinction rates identified by MacArthur and Wilson were area and isolation. Reasoning that larger islands would have larger populations and thus lower extinction rates, and that more isolated islands would have lower immigration rates, they generated a number of predictions in accord with empirical observations. In particular, islands of larger area were expected to support more species than smaller islands.

This conclusion, that species number should increase with increasing island area, was also reached by Preston (1962), who proposed an equation for the species-area curve. By regarding larger islands as having larger numbers of individuals, and by assuming a lognormal species-abundance distribution on all islands, Preston derived the approximate form of the species-area relationship as

$$S = CA^z \quad (1),$$

where S is the number of species, A is area, C is a constant related to population density, and z is a constant. This equation is an approximation of the actual theoretical relationship between S and A, which is not a simple function (May 1975). Preston arrived at the power function approximation by fitting theoretical points to a line by least squares regression. The power function form was chosen for convenience and good fit over a reasonable range of S and A.

Species-area theory, both in the formulation of MacArthur and Wilson (1963, 1967) and that of Preston (1962), rests on the fundamental assumption that increasing island areas allow increased population sizes. However, it is clear that area itself usually has no direct effect on organisms, and that area is in fact a convenient secondary correlate which measures more proximate factors. Two such factors are frequently mentioned: first, increased area implies a greater total amount of habitat, and so a greater total amount of resources, capable of supporting larger populations. Second, larger islands or insular areas may contain a greater variety of habitats or resource types, thus supporting populations of a greater variety of species (MacArthur and Wilson 1967, MacArthur 1972: 102, Connor and McCoy 1979, Brown 1981). In both cases energy, in the form of resources, is a parameter of interest.

The accuracy of area as a measure of either the total amount of resources or the variety of resource types available depends on the set of islands examined. In general, area is accurate if the islands are fairly uniform in their climate, topography, and geology (Preston 1962, MacArthur and Wilson 1967: 8, 13), but is less satisfactory when the islands are varied in these respects (Johnson et al. 1968, Power 1972, Johnson 1975). In order to extend the species-area models to apply more generally, then, it is necessary to adopt a more direct measure of the important proximate factors than area provides. I will present a modification of the models of Preston and MacArthur and Wilson that replaces the area parameter with available energy, explore the implications of the theory resulting from this replacement, which I have called species-energy theory, and present relevant data for angiosperms and land and freshwater birds on islands. The potential for using these concepts to predict species occurrence and abundance as well as the number of species on an island, and the value of the theory in providing a unified basis for interpreting diverse observations, are also discussed.

## The meaning of available energy in species-energy theory

Species-energy theory is obtained essentially by replacing "area" with "available energy" in the models of MacArthur and Wilson (1963, 1967) and Preston (1962). This substitution is illustrated in the following section. This section explains the meaning of available energy and why its placement in these models is desirable. The estimation of available energy in practice is discussed in the section "Testing species-energy theory".

Available energy on an island is the rate at which resources available to the species of interest are produced on the island as a whole. In other words, available energy measures the total amount of available resource production on an island, which is one of the likely proximate factors affecting species population sizes. Area can only measure total available resource production accurately when the per-unit-area productivity of different islands is similar.

Available energy, like area, does not directly measure the variety of resource types present on an island, but is



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correlated with it. That is, the larger the total resource production on an island, the greater the variety of resource types is likely to be.

Thus available energy serves as a more general measure of total resource production on an island than does area, and also provides some information on the variety of resource types present. Species-energy theory should therefore prove more general than species-area theory, particularly by being applicable to islands which vary in their per-unit-area resource productivity, due to factors such as climate, topography, or soil chemistry.

### The effect of available energy in the equilibrium model, and species-energy curves

The equilibrium theory of available energy and species number is completely analogous to the MacArthur-Wilson model (1963, 1967). The number of species on an island is represented as the result of a dynamic immigration-extinction process, and, following MacArthur and Wilson, I assume that smaller populations are more likely to suffer extinction (see also Jones and Diamond 1976, Terborgh and Winter 1980, Leigh 1981). If the island as a whole produces little energy that is available to the species in question, then species population sizes will be small, and the extinction rate on the island will be high. On the other hand, islands with large amounts of available energy will support larger populations of all species, and so will have lower extinction rates. Thus available energy has the same effect on extinction rate that MacArthur and Wilson proposed for area. Also, like area, available energy should often have negligible effect on immigration rates. For islands of similar isolation, then, the islands with greater available energy will have higher equilibrium species numbers. Fig. 1 presents the familiar graphical representation of this result.

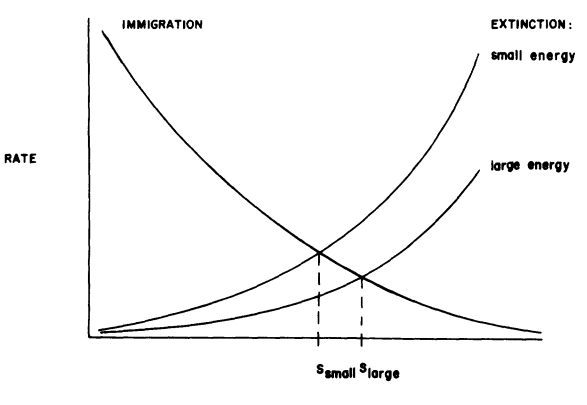


Fig. 1. Immigration and extinction rates versus number of species present on an island. Islands with larger total amounts of available energy have lower extinction rates, resulting in a higher equilibrium number of species ($S_{large} > S_{small}$).

By assuming that a specific form of species-abundance distribution holds on all islands, it is possible to derive a more precise, though possibly less general, form of the relationship between available energy and species number, analogous to the species-area curve derived by Preston (1962; see May 1975 for a more exhaustive treatment). Some interesting ties exist between species-energy and species-area curves.

A basic assumption in Preston's formulation of the species-area curve was that the total number of individuals of all species on an island should be proportional to its area, i.e., that $N = \delta A$, where $\delta$ is the total density of individuals per unit area. Similarly, I assume here that the total number of individuals on an island, N, is proportional to the total production of available energy on the island, E, i.e.,

$$N = \varrho E$$

where $\varrho$ is the number of individuals supported per unit of available energy. That $\varrho$ is geographically constant for a given taxonomic group must be subject to empirical test. For the present I will assume that it is constant. The predicted form of the species-energy curve is then approximately (Preston 1962, May 1975)

$$S = kE^z \qquad (2)$$

where k is a constant related to $\varrho$, and S and z are as in Eq. (1).

In the species-area relation (1), the coefficient C is shorthand for

$$C = b\left(\frac{\delta}{m}\right)^z$$

where b is a fitted constant from the power function approximation to the theoretical species-area relationship, and m is the population size of the rarest species (Preston 1962). The constant k, on the other hand, is

$$k = b\left(\frac{\varrho}{m}\right)^z.$$

C and k are closely related. If we let r be the per-unit-area productivity of available energy on an island, then, since $\varrho r = \delta$,

$$C = kr^z \qquad (3).$$

This implies that C should vary with per-unit-area productivity, as has been previously suggested (MacArthur and Wilson 1967: 17), and that if we examined C values from species-area curves for a given taxonomic group and compared these with the per-unit-area productivity values for the corresponding sets of islands, we would expect the linear relationship

$$\log C = \log k + z \log r$$



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This makes good sense, since C is larger under conditions where δ, the total density of individuals, is higher; and the total density of individuals is generally higher where the per-unit-area productivity of the habitat is higher. Connor and McCoy (1979) provided an indirect test of this prediction by correlating C values, as well as mean number of species for sets of islands (which differs from C for a given sets of islands only due to choice of units for area, see Gould 1979), with latitude. Unfortunately, latitude is not a very accurate indicator of per-unit-area productivity of available energy. Most of the correlation coefficients calculated by Connor and McCoy were non-significant but negative; a significant negative correlation was found between latitude and mean number of species for birds. In any collection of data, a possible relationship between C and r could be obscured by differences in the isolation, ranges of area covered, and differing z values of different sets of islands.

The relationship suggested by Eq. (3) can be restated in a more qualitative, intuitive way: among islands of similar isolation, islands with low per-unit-area productivity are expected to fall below islands with higher productivity in a logarithmic plot of species number against area. This is what Lassen (1975) found for snails in oligotrophic and eutrophic lakes.

The relationship between C and r also suggests an alternative method of conceptualizing the species-energy curve. Think of a graph of log S versus log A on which sets of islands differing in their per-unit-area productivity of available energy (r) are plotted. For the sake of argument, assume that the slopes of the various species-area curves are approximately the same. Then these relations plot as more or less parallel lines with slopes of about z, with sets of islands with higher r above those of lower productivity (Fig. 2). Their higher C, the log of which is the intercept on the log S axis, reflects this arrangement. If log S were instead plotted against log E = log A + log r, each line would be shifted rightward by an amount log r. Since the higher lines are shifted correspondingly more to the right, this results in the separate species-area curves coalescing into a single species-energy curve.

In both the equilibrium model and species-energy curves, species-area theory appears as a special case of species-energy theory. When islands of similar per-unit-area productivity are examined, area serves as an excellent relative measure of available energy, and the species-energy models collapse to the species-area models of MacArthur and Wilson and Preston. Thus species-energy theory does not require the abandonment of species-area investigations, nor does it necessarily invalidate the use of area as a parameter. For the purposes that it has served to date, namely the comparison of islands with similar per-unit-area productivity, species-area theory is completely valid.

To summarize at this point, species-energy theory recognizes available energy as a proximate factor affecting species population sizes. Many of the predictions made by MacArthur and Wilson and by Preston apply to species-energy theory, since available energy can easily be substituted for area in both models. Doing so results in the following qualitative and quantitative predictions: it should be possible to compare islands differing radically in their per-unit-area productivity of available energy and area, and among islands of similar isolation, islands with greater amounts of available energy should support more species than islands with less available energy. More precisely, if species-abundance distributions on islands are lognormal and of similar form, we expect the approximate relationship $S = kE^z$. If many species-area relationships of island groups of similar isolation are examined, the coefficient C of the species-area curve should vary with per-unit-area productivity according to the relationship $C = kr^z$. Species-area theory continues to be interesting and useful, and is contained as a special case within species-energy theory.

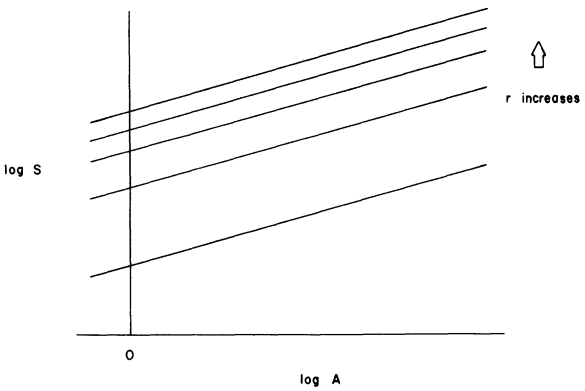


Fig. 2. Hypothetical species-area curves for islands of similar isolation but different per-unit-area productivity of available energy (r).

## Testing species-energy theory

Testing the predictions of species-energy theory usually involves the problem of measuring available energy. The predictions of Eqs (2) and (3), in particular, rely on this quantity.

Available energy should be estimated by considering what amount of energy production in general on an island is available to a given group of species, due to the unique requirements and constraints of that group. For example, a measurement of energy available to plants might recognize solar energy as the ultimate source of plant energy, and then also take into account constraints on the usability of raw solar energy due to factors such as lack of water or nutrients. Energy available to animals consists of the production of food items that can be included in the diets of the group in question.



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Tab. 1. Number of species of angiosperms and breeding land and freshwater bird on islands worldwide.

| Island | Location | Area ($10^3$ km$^2$) | Average AET[a] (cm yr$^{-1}$) | Average NPP[b] (kg m$^{-2}$ · yr$^{-1}$) | Total AET[c] (km$^3$ yr$^{-1}$) | Total NPP[d] ($10^9$ t yr$^{-1}$) | Number of[e] angiosperms | Number of[f] birds |
|---|---|---|---|---|---|---|---|---|
| 1. Australia | 25°S, 135°E | 7705 | 55 | 0.6 | 4240 | 4.62 | 12,000 | 529 |
| 2. New Guinea | 5°S, 142°E | 809 | 125 | 2.3 | 1010 | 1.86 | 9000 | 540 |
| 3. Borneo | 0°, 115°E | 751 | – | 2.0 | – | 1.50 | – | 420 |
| 4. Madagascar | 20°S, 47°E | 591 | 88 | 1.5 | 517 | 0.89 | 6000 | 184 |
| 5. Philippines | 11°N, 123°E | 300 | 125 | – | 375 | – | 7620 | – |
| excluding Palawan | | 288 | – | 2.1 | – | 0.60 | – | 325 |
| 6. Japan | 37°N, 139°E | 359 | 63 | 1.1 | 226 | 0.39 | 3417 | 216 |
| 7. Sulawesi | 2°S, 122°E | 179 | – | 2.1 | – | 0.38 | – | 220 |
| 8. New Zealand | 42°S, 173 E | 269 | 63 | – | 169 | – | 1725 | – |
| 9. Java | 7°S, 110°E | 124 | – | 2.1 | – | 0.26 | – | 337 |
| 10. Cuba | 22°N, 79°W | 114 | 125 | 1.7 | 143 | 0.19 | 8000 | 124 |
| 11. Britain | 54°N, 2°W | 230 | 50 | 1.1 | 115 | 0.25 | 1730 | 172 |
| 12. Hispaniola | 19°N, 71°W | 76 | – | 1.7 | – | 0.13 | – | 106 |
| 13. Sri Lanka | 7°N, 81°E | 66 | 88 | 1.8 | 58.1 | 0.12 | 3000 | 235 |
| 14. Taiwan | 24°N, 121°E | 36 | 125 | – | 45.0 | – | 3265 | – |
| 15. Tasmania | 42°S, 147°E | 67 | 63 | – | 42.2 | – | 1200 | – |
| 16. Solomon Is. | 7°S, 157°E | 30 | 125 | – | 37.5 | – | 1650 | – |
| 17. Iceland | 65°N, 18°W | 103 (85[g]) | 38 | – | 32.3 | – | 375 | – |
| 18. Ireland | 53°N, 8°W | 84 | 38 | 1.1 | 32.0 | 0.092 | 1200 | 108 |
| 19. Timor | 9°S, 125°E | 34 | – | 2.0 | – | 0.068 | – | 137 |
| 20. Newfoundland | 48°N, 56°W | 112 | – | 0.6 | – | 0.067 | – | 103 |
| 21. Baffin | 68°N, 73°W | 476 (453) | 7 | 0.1 | 31.7 | 0.045 | 261 | 40 |
| 22. Sakhalin | 50°N, 142°E | 78 | 38 | – | 29.6 | – | 1166 | – |
| 23. Greenland | 73°N, 40°W | 2176 (384) | 7 | – | 26.9 | – | 400 | – |
| 24. Vancouver | 49°N, 126°W | 32 | – | 1.2 | – | 0.038 | – | 124 |
| 25. Flores | 9°S, 121°E | 17 | – | 2.1 | – | 0.036 | – | 143 |
| 26. New Caledonia | 20°S, 165°E | 19 | 100 | 1.8 | 19.0 | 0.034 | 2600 | 68 |
| 27. Fiji | 17°S, 178°E | 18 | 100 | 1.8 | 18.0 | 0.032 | 1250 | 61 |
| 28. Palawan | 10°N, 118°E | 12 | – | 2.1 | – | 0.025 | – | 131 |
| 29. Sumba | 10°S, 120°E | 11 | – | 2.0 | – | 0.022 | – | 103 |
| 30. Victoria | 71°N, 110°W | 212 | 7 | 0.1 | 14.8 | 0.021 | 222 | 43 |
| 31. Jamaica | 18°N, 77°W | 12 | 100 | 1.7 | 12.0 | 0.020 | 2888 | 99 |
| 32. Ellesmere | 80°N, 80°W | 196 (108) | – | 0.1 | – | 0.011 | – | 22 |
| 33. Banks | 73°N, 120°W | 64 | – | 0.1 | – | 0.0064 | – | 34 |
| 34. Falkland Is. | 52°S, 59°W | 16 | 32 | 0.4 | 5.1 | 0.0064 | 170 | 33 |
| 35. Novaya Zemlya | 74°N, 56°E | 83 (62) | 7 | – | 4.3 | – | 200 | – |
| 36. Spitsbergen | 78°N, 20°E | 61 (25) | 7 | 0.1 | 1.7 | 0.0025 | 137 | 9 |

a. Average actual evapotranspiration, in cm of water per year. Estimated from Lieth (1975) for ice-free areas.
b. Average net primary productivity, in kg of dry matter per m$^2$ per year. Estimated from Lieth (1975) for ice-free areas.
c. Obtained by multiplying average Aet by the area of the island free from permanent ice cover.
d. Obtained by multiplying average NPP by the area of the island free from permanent ice cover.
e. From Good (1974), except 5 (Merrill 1926), 6 (Numata 1974), 21 and 30 (Porsild 1957), and 31 (Adams 1972).
f. From Pizzey (1980), Rand and Gilliard (1967), Delacour and Mayr (1946), Moreau (1966), Anon. (1975), Preston (1962), Parslow (1973), Godfrey (1966), Mayr (1945), Woods (1975), and Løvenskiold (1963).
g. In parentheses is area free from permanent ice cover. From Encyclopædia Brittanica or estimated from maps.



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Ideally, available energy would be measured in units of energy per unit time, e.g. joules per year. However, in practice, any relative measure of available energy can serve, as long as it bears a consistent proportionality to available energy for the set of islands examined. The units of a relative measure will not necessarily be those of energy/time. A disadvantage of using a variety of relative methods to estimate available energy is that the use of different units precludes certain comparisons between data sets, such as comparison of intercept values.

To test the generality of the equation $S = kE^z$, I have compiled data on the number of species of angiosperms and of land and freshwater birds on islands worldwide (Tab. 1). All world islands with areas greater than $10^5$ $km^2$, for which data on species numbers of angiosperms or land and freshwater birds were available to me, were tabulated; with the exception that several islands in the Canadian arctic archipelago were excluded, in order to avoid over-representation of these high latitude islands in the sample, and because many are not well-explored.

For both angiosperms and birds, relative measures of available energy were used. For angiosperms, actual evapotranspiration (AET) was used to produce a measure of energy available to plants. Despite its name, AET does not involve actual measurements of evaporation or transpiration rates, but is calculated from climatic data for any particular site. AET estimates total incident solar energy by mean monthly temperatures above 0°C, and corrects for the amount of this energy which is unavailable to plants due to lack of water by taking into account monthly mean precipitation and standardized estimates of evaporation, transpiration, and soil water storage (Major 1963, Rosenzweig 1968). Its utility is demonstrated by the observation that AET is the best known single predictor of global patterns of terrestrial primary productivity (Lieth 1975).

To estimate available energy for angiosperms, total AET (TAET) for an island was calculated by multiplying the annual rate of AET, averaged over the whole island, by the area of the island. Annual AET rates, in cm $H_2O$ $yr^{-1}$, were obtained from a global map of AET developed by E. Box (Lieth 1975). TAET, in $km^3$ $H_2O$ $yr^{-1}$, is plotted with angiosperm species number on logarithmic coordinates in Fig. 3. The resulting relationship is fit by the curve $S = 123\ (TAET)^{0.62}$, explaining 70% of the variation in the logarithm of angiosperm species number. Island area does not explain a significant proportion of the variance ($S = 475\ A^{0.26}$, A in $10^3$ $km^2$, $r = 0.26$, $P > 0.05$), and the fit obtained using log TAET is significantly better (test for equality of correlation coefficients, $t = 2.88$, $P < 0.005$; Sokal and Rohlf 1969: 521).

For land and freshwater birds, total net primary production (TNPP) was used as a relative measure of available energy. TNPP was estimated by multiplying the average per-unit-area net primary productivity on the island, in kg dry matter · $m^{-2}$ · $yr^{-1}$ (Lieth 1975), by the area of the island. Regressing log S on log TNPP yields the relation $S = 358\ (TNPP)^{0.47}$, TNPP in $10^9$ t dry matter $yr^{-1}$, explaining 80% of the variation in log S (Fig. 4). The species-area regression is significant in this case ($S = 32.8\ A^{0.27}$, $r = 0.44$, $P < 0.05$), but area again explains significantly less of the variance in species number ($t = 3.35$, $P < 0.001$).

In both plots, islands at high latitudes, which are

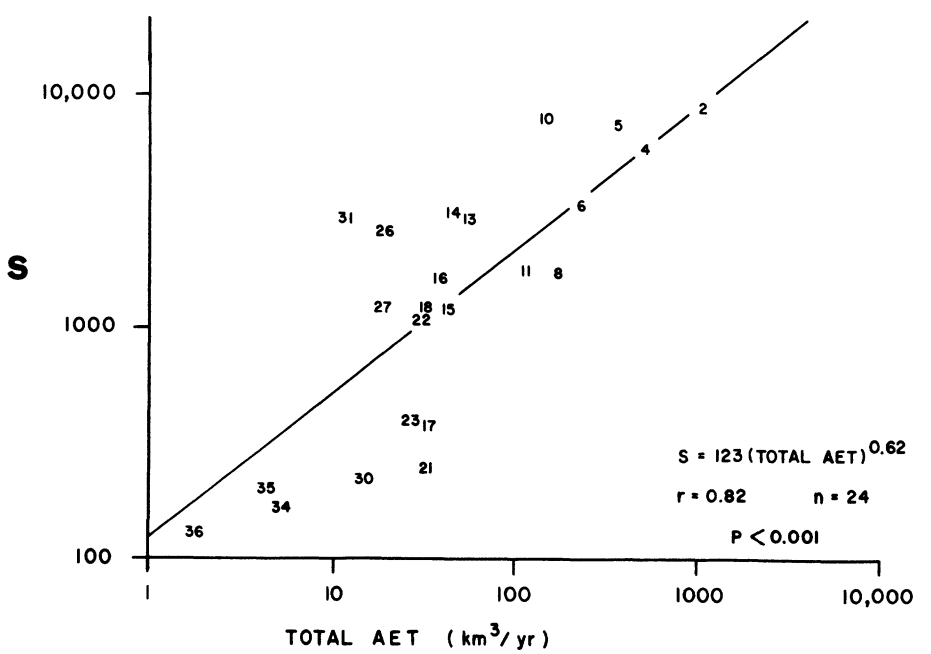


Fig. 3. Number of angiosperm species (S) on 24 islands worldwide, plotted against the total actual evapotranspiration (Total AET) from the island annually. Numbers in the plot refer to islands listed in Tab. 1.



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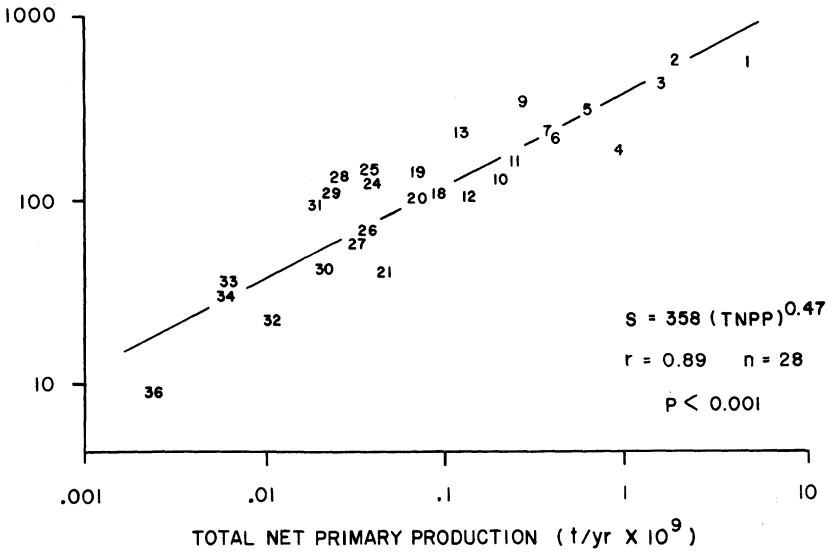


Fig. 4. Number of breeding land and freshwater bird species (S) on 28 islands worldwide, plotted against the total net primary production on the island annually, in billions of metric tons of dry matter. Numbers in the plot refer to islands listed in Tab. 1.

typified by low per-unit-area rates of AET and net primary productivity, still tend to have lower species numbers than islands with the same TAET or TNPP but with higher per-unit-area rates. There are many possible interpretations of this result, for example:

1) It may be that TAET and TNPP are not consistently proportional to available energy, but overestimate it for low per-unit-area productivity habitats.
2) It may be that ϱ, the number of individuals supported per unit of available energy, is not constant, but decreases with decreasing r.
3) Species-abundance distributions may differ in form in areas with different r. For example, if the standard deviation of lognormal species-abundance distributions increases in low per-unit-area productivity environments (Preston 1980), then z values for these environments will tend to be lower (May 1975: eq. A16, Schoener 1976, Martin 1981). This will result in the failure of species-area curves to coalesce in a species-energy plot, with the species-energy curves of low-r islands falling below those of high-r islands.
4) It might be that the low species diversity of the source pools for high latitude islands depresses their equilibrium species number. If this is the case, we would expect the depression to be more marked on larger islands.

All of these possibilities are quite amenable to empirical test, and suggest the existence of interesting geographical patterns in resource utilization and species-abundance distributions. In any case, it should be noted that the combined tendency of low per-unit-area productivity islands to fall below and to the left of high productivity islands in Figs 3 and 4 probably has artificially increased the estimates of z.

In both examples in this section, a relative rather than a direct measure of available energy was used, and this will often necessarily be the case in tests of species-energy theory. However, it is also possible to identify situations in which direct measurements of available energy could be made. Freshwater ecosystems seem most promising; for instance, species number of zooplankton could be compared with available energy in lakes and ponds, by converting measurements of total net primary production to units of energy/time. Such a comparison would be especially relevant to species-energy theory if variation in per-unit-area productivity among the lakes and ponds, due to oligotrophy, eutrophy, or factors such as elevation, were large. In terrestrial ecosystems, total net primary production, again converted to energy/time, may provide a first order estimate of available energy for herbivorous insects. Available energy for web-building spiders or bats could perhaps be estimated using insect light-trap data.

The attempts to apply species-energy theory that I have presented in this section have shown that available energy can be used to explain variation in species number when islands with widely different physical environments are compared. In addition, the specific quantitative prediction that the species-energy curves of different sets of islands should fall on a single line has apparently been falsified. This falsification has suggested some interesting questions, investigation of which could potentially lead to a refinement of the theory, and to a greater understanding of general patterns of diversity.

## Discussion

The concepts embodied in species-energy theory and equilibrium biogeography can potentially be used not



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only to predict patterns of species number but also to address in detail the abundances of individual species on islands and their probabilities of being present or absent. To do so naturally requires more detailed information about individual species and islands than is necessary merely to predict a rough species number. Predicting species abundances and probabilities of occurrence will require, at least, knowledge about individual species' resource requirements and about the production of resources on islands.

Detailed information about the total production on an island of resources available to a particular species; which would ideally include some consideration of how much was unavailable due to physical environmental conditions, competitors, and predators; and about the resource requirements of individuals of the species, would allow an estimation of the species' abundance if present. To oversimplify, a species should be abundant if it has abundant available resources on an island.

Because of the assumed relationship between population size and extinction rate, the abundance that a species can maintain should affect the probability that it will occur on an island. Simberloff (1969) suggested that the probability that a species A occurs on an island is

$$\Pr(A) = \frac{1}{1 + \frac{E_A(n)}{I_A(d)}} \qquad (4)$$

where $I_A(d)$ is A's immigration rate and $E_A(n)$ is A's extinction rate when present on the island. I have indicated that $I_A$ is a function of the distance, d, of the island from sources of immigrants, while $E_A$ is a function of the population size, n, that A can maintain on the island (Jones and Diamond 1976, Terborgh and Winter 1980). For any particular species the forms of I(d) and E(n) would have to be measured to obtain explicit probabilities of occurrence; however, qualitative predictions about relative probabilities of occurrence can easily be made by comparing the magnitudes of the ratio I/E for different species or taxa (Wright 1981).

In essence, species-energy considerations lead to the expectation that a species with abundant resources on an island should be both more abundant on the island if it does occur and, consequently, more likely to occur than an equally dispersive species with few resources.

These notions about the occurrence and abundance of species, in conjunction with the equilibrium and species-energy curve models of species-energy theory, provide a framework that unifies a broad set of observations of patterns in species diversity. None of these observations are new, and some of the patterns are so intuitive that there seems little need for a theoretical explanation. The virtue of the theory in such instances lies in its ability to interrelate previously unconnected observations, and to point out new areas of interest and new avenues of approach. I will briefly list some of the observations of diversity patterns for which species-energy theory may provide an explanation.

*The diversity of trophic levels.* Due to the progressive diminution of available energy at higher trophic levels, species-energy theory predicts that lower trophic levels should be more diverse; for example, on any given island there should be more herbivores than carnivores. An examination of Tab. 1 shows that birds are always less diverse than angiosperms on any island. This is consistent with species-energy theory, since all birds are at least 1 trophic level above angiosperms. Such ideas date as far back as Elton's early discussion of the pyramid of numbers (1927). This prediction is not exact, but interacts with the factors discussed below.

*Metabolic requirements and diversity.* Other things being equal, species with greater metabolic requirements should in general be less diverse, less abundant, and occur less frequently than species with lower requirements. Because total metabolic rate scales approximately as body mass to the power of 0.75 for organisms ranging from homeothermic and poikilothermic vertebrates to trees and bacteria (Schmidt-Nielsen 1979: 186), species-energy theory may serve as a partial explanation for the observed size-diversity relationship (Van Valen 1973, May 1978); that is, why small organisms are roughly 100 times as diverse as similar organisms 10 times their length. (For example, assuming no bias in the amount of energy available to organisms of different sizes in a habitat, the environment would supply $10^{0.75}$ times as many individual-equivalents of energy to organisms weighing 1 g as to those weighing 10 g, implying a species-supporting capacity $(10^{0.75})^z$ times as great for the smaller organisms.) Species of large body size or high metabolic requirement are often among the first to be extirpated from newly formed islands or habitat areas reduced in size (Brown 1971, Willis 1974, Terborgh and Winter 1980, Wright 1981).

It is tempting to use this argument to compare homeothermic and poikilothermic vertebrates; however, these groups differ greatly and with systematic biases in other important respects, such as the resources available to them, their susceptibility to predation, their response to climatic conditions, and their potential for immigration, so that such comparisons will be difficult to interpret (but see Wilcox 1980, Wright 1981).

It is interesting to note that the effect of body size is likely to interact with the effect of trophic level. Lindemann (1942) suggested that the relative sizes of producers and consumers would be of profound importance in understanding ecosystems. In marine ecosystems, the producers are small and primary consumers typically somewhat larger, whereas in terrestrial systems producers are much larger, and primary consumers may be considerably smaller than the organisms they consume. This may in part account for the diversity of herbivorous



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Tab. 2. Frequency of occurrence and average population density, when present, of crustacean zooplankters in 34 lakes in northwestern Ontario (from Patalas 1971, 1968 sample data). Spearman rank correlation $r_s = 0.53$, $P < 0.05$.

| Species | Average population density ($cm^{-2}$) | Frequency of occurrence (No. lakes present/34) |
|---|---|---|
| 1. *Cyclops bicuspidatus* | 17.17 | 0.59 |
| 2. *Diaptomus minutus* | 9.61 | 0.68 |
| 3. *Diaptomus sicilis* | 5.79 | 0.12 |
| 4. *Orthocyclops modestus* | 4.56 | 0.12 |
| 5. *Diaptomus oregonensis* | 2.86 | 0.26 |
| 6. *Mesocyclops edax* | 2.43 | 0.71 |
| 7. *Tropocyclops prasinus* | 2.38 | 0.76 |
| 8. *Diaptomus leptopus* | 2.02 | 0.15 |
| 9. *Daphnia retrocurva* | 1.84 | 0.26 |
| 10. *Cyclops vernalis* | 1.83 | 0.24 |
| 11. *Bosmina longirostris* | 1.73 | 0.88 |
| 12. *Diaphanosoma leuchtenbergianum* | 1.54 | 0.47 |
| 13. *Daphnia catawba* | 1.43 | 0.15 |
| 14. *Daphnia galeata* | 1.37 | 0.35 |
| 15. *Chydorus sphaericus* | 1.21 | 0.18 |
| 16. *Diaphanosoma brachyurum* | 1.16 | 0.38 |
| 17. *Holopedium gibberum* | 0.86 | 0.68 |
| 18. *Daphnia longiremis* | 0.60 | 0.06 |
| 19. *Epischura lacustris* | 0.36 | 0.47 |
| 20. *Ceriodaphnia lacustris* | 0.24 | 0.15 |
| 21. *Senecella calanoides* | 0.23 | 0.06 |
| 22. *Daphnia schoedleri* | 0.19 | 0.03 |
| 23. *Limnocalanus macrurus* | 0.09 | 0.09 |
| 24. *Ceriodaphnia pulchella* | 0.07 | 0.03 |
| 25. *Leptodora kindtii* | 0.02 | 0.21 |
| 26. *Streblocerus serricaudatus* | 0.004 | 0.03 |

insects being greater than the diversity of their plant hosts. Insect parasitoids also constitute an interesting case.

*Rarity and patchy distribution.* Eq. (4) implies that rare species (species which have low abundance when they occur), because they are more prone to extinction events, should occur less frequently than more abundant species on a large set of islands. Tab. 2 demonstrates this relationship for crustaceans in lakes in northwestern Ontario; Diamond (1980) suggests that this is also qualitatively the case for New Guinea birds. Species may be rare for a great variety of ecological reasons, such as susceptibility to predators, competitors, or environmental conditions, or rarity of requisite resources on the island. Several authors have previously suggested a relationship between extreme resource specialization and species extinction rates (Connell and Orias 1964, Brown 1971, 1978, Willis 1974, Terborgh and Winter 1980).

*Seasonal variation in diversity.* As would be predicted by species-energy theory, seasonal trends in diversity mirror seasonal trends in energy availability (Connell and Orias 1964, Shapiro 1975). This pattern is especially marked in the temperate zones, where many birds emigrate, and many mammals, reptiles, amphibians, insects, and plants enter periods of dormancy.

*Latitudinal diversity gradients.* Species-energy theory would predict latitudinal gradients in diversity if lower latitudes were also characterized by greater total available energy. As mentioned above, a rough correlation exists between latitude and measures of per-unit-area productivity, such as AET and net primary productivity (Lieth 1975). Terborgh (1973) has argued that the area of low latitude habitats is also much greater than that of high latitude habitats, but this is less than clear for regions such as central America and northern tundra and taiga. Quantitative estimates of habitat areas and productivity are needed to address this question.

Finally, a comment on the applicability of species-energy theory is in order. As presented here, species-energy theory assumes that the population size of a group of species in an insular habitat is affected by the total amount of available energy production (i.e. $\partial N/\partial E = \varrho$, $\varrho > 0$). In some cases this may not be true, for example, fishes on coral reefs or seabirds on high latitude islands might be so severely limited by the availability of hiding holes or nesting sites that available energy has no effect on the number of individuals in the community. A simple experimental test of this assumption would be to see whether the number of individuals in the community changed in response to an increased or decreased food supply. Overall, however, it is clear that species-energy theory lacks universal applicability



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in that energy need not necessarily affect population sizes. While it might be possible in any particular instance to identify the most important non-energetic factors affecting a community's population size and so its species number, these factors vary from place to place and with the taxa being considered; thus such an approach lacks the generality of species-energy theory in explaining geographic patterns in species diversity. Ideally, we seek a "species-limiting factors" theory which can both account for a variety of factors, potentially including energy, that affect population sizes; and apply across taxonomic and geographic distances. Species-energy theory is only a step in this direction.

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