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A System in Which Available Energy Per Se Controls Alpha Diversity: Marine Pelagic Birds

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ABSTRACT: An attractive explanation for large-scale gradients of species richness is that trophic energy flux defines living systems. It has yet to be shown that available energy may matter per se, that is, directly and independent of other potential determinants that are usually inescapably correlated (e.g., area, glacial history, or habitat complexity). By using a comprehensive conceptual framework addressing the variation of species richness, we report that in communities of birds regularly foraging in marine pelagic waters during the breeding season, species richness is above all directly linked to the appropriation of metabolic energy. Auxiliary energy supplied by wind and waves is likely to mitigate energetic constraints and thereby codetermine the expansion of niche space, along with an array of other subordinate factors. We emphasize that this system is markedly different from studied communities of terrestrial endotherms or marine exotherms in which habitat complexity and mutagenic solar radiation/temperature, respectively, may be more decisive than the appropriation of trophic energy flux shares as such. While the seabird system suggests that species-energy curves may sometimes directly translate into species-energy relationships, this situation may be rare rather than typical.

Keywords: ecological communities, available energy, species richness, alpha diversity, seabirds.

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Since consecutive generations of organisms can be seen as transmitters and receivers of mutable germline information, living systems match Shannon's (1948) information concept and can be understood as information flux through time. Organisms steadily have to degrade available energy (Boltzmann 1886) in order to maintain and amplify the information of the lineages they represent. Both evolutionary history and the environment (Kleiber 1931; Sewertzoff 1934 as quoted by Zotin and Lamprecht [1996]) rule the metabolic rate as a broadly understood, modernage vis vitalis maintaining information by keeping organisms away from the thermodynamic equilibrium of the inanimate environment. On theoretical as well as empirical grounds, it is reasonable to assume that the limitation of species richness and/or the pace of diversification may to some extent be under the control of the supply of available energy (Wright 1983; Adams and Woodward 1989; Currie 1991; Bambach 1993; Guégan et al. 1998; Waide et al. 1999; Hawkins et al. 2003). On the other hand, it is usually impossible to unravel whether available energy is relevant as such, because a number of alternative potential determinants of species richness related to equally reasonable ideas are often highly correlated with available energy and are likely to predict patterns very similar to those expected on energetic grounds. For example, on land, local primary productivity, as a good approximation of the biochemical fixation of available energy of whole communities, increases with global area at a given latitude (while the northern and southern tropics are contiguous, contrary to other climatic zones; Terborgh 1973), geometric and physical habitat complexity created by the aboveground vegetation (Horn 1971), the extent and immediate impact of Plio-Pleistocene glaciations (Adams and Woodward 1989), as well as former landmass distributions that might still affect patterns observed today (Wiens et al. 2006).

So far, the studies reporting high correlations between energy supply and species richness are exploratory; they allow hypotheses to be formulated but do not seriously scrutinize whether available energy is causal. Any attempt to dissect a species-energy relationship first has to demonstrate that it is not just a curve that can always be plotted

regardless of whether energy supply is proximately causal. Because the terms "energy" and "available energy" can be used correctly in several different ways, and some semantic trouble exists in the published literature, we define available energy and the associated hypothesis on species richness in appendix A in the online edition of the *American Naturalist*.

Geographic patterns of biodiversity are beyond the scope of controlled experiments (which cannot apply to large areas or macroevolutionary timescales). The only way to leave the purely exploratory stage is to replace the control of the experiment with a comprehensive conceptual framework and scan the biosphere for situations in which it is possible to restrict the number of parameters that may produce a given pattern. Causal inference by this approach goes along with a reduction of internal validity in favor of external validity. The former denotes the strength of the experimental and statistical design, and the latter denotes the relevance of a given result in the real world. To assess the validity of hypotheses and separate determinants (causal parameters) from predictors (parameters allowing phenomenological prediction, regardless of whether these are causal) and correlates (associations that need not even permit prediction), situations are needed in which the prediction based on the target parameter (related to the target hypothesis, which is thought to apply to the system) deviates from the patterns that might have been brought about by alternative hypotheses of the conceptual framework.

The Seabird System

A system that has been considered for the identification of energetic constraints imposed on biodiversity is given by seabird communities (Hashmi 1998, 2002), in which species richness is known not to decrease monotonically with increasing latitude (Udvardy 1974). Here we focus more specifically on species regularly foraging in marine pelagic waters during the breeding season. This set of species forms a clearly defined guild of land-breeding, endothermic, and air-breathing marine predators that exploit the uppermost layers of marine pelagic waters from the surface. It is ecologically distinct from pelagic pinnipeds as the most similar guild, differing by purely aquatic locomotion, larger body mass, and associated capacities of oxygen (Halsey et al. 2006) and energy storage. Comprising 290 species (Del Hoyo et al. 1992, 1994, 1996), the set is large enough to be statistically informative and small enough not to represent a confusing myriad of lineages that are ecologically difficult to trace. Some seabird species that forage in pelagic habitat during the breeding season also obtain food in benthic, littoral, limnic, or terrestrial habitats, but enough is known to consider feeding

habitat. Moreover, it is possible to partition continental coastlines with a spatial resolution that widely allows the exclusion of breeding habitat limitation as well as lumping of para- or allopatric species that replace each other along continuous or contiguous seascapes. Just as alpha diversity of forest birds may include species of different strata along a gradient from the ground to the space above the treetops that do not necessarily breed where they forage, alpha diversity of seabird communities denotes species that commute to pelagic waters along a gradient from coastal to oceanic habitats. In both cases, alpha diversity is not restricted to species foraging syntopically. Contrary to forest birds, which nest in all except the highest strata of the space that may be used as foraging habitat, seabirds commute to pelagic waters from a comparatively narrow margin of terrestrial breeding habitats not too far away from the coast.

Defined like this, the alpha diversity of seabird communities meets several prerequisites that are needed to identify energetic constraints. First, seabirds are not restricted to a limited part of the marine realm but exist throughout the whole range of climatic conditions found at the surface of the seas. Whereas primary production on the continents is dominated by the supply of water and solar radiation (Currie 1991), in the oceans it is typically limited by the availability of nutrients. As a consequence, there is no monotonic change of marine pelagic annual net primary production with increasing latitude and no inevitable coupling of energetic and alternative determinants of species richness in the oceans. Second, seabirds are among the most mobile and itinerant organisms found on earth (Shaffer et al. 2006). Although individuals of many species are markedly philopatric, especially those able to forage in oceanic waters far away from their colonies during reproduction, seabird populations, including flightless species, are known to be capable of responding to climatic changes with latitudinal shifts of their breeding distributions (Mourer-Chauviré and Antunes 1991). Although prey choice is not random in most species and the quality of prey does not depend merely on its gross energetic content (Roby 1991), most species, especially those with restricted foraging ranges, are generalists and face considerable variation in the availability of different types of prey. Third, the extent of the habitat where nonbreeding oceanic seabirds may forage is much greater than the extent of the waters that commuting adults may use when breeding. Therefore, in communities of breeding seabirds, density dependence related to available energy as a limiting resource is a strong evolutionary force in the tropics (Ashmole 1963) as well as at higher latitudes (Furness and Birkhead 1984). Although strong intraspecific density dependence does not necessarily beget interspecific density dependence, it renders the exclusion of species by diffuse

competition more likely. Fourth, since breeding seabirds can easily be captured and recaptured at their nest sites, they are well represented among the species for which field metabolic rates have been measured (Nagy et al. 1999). Fifth, at sea, seabird life mainly takes place between 200 m above and below the surface in a comparatively simply structured habitat that, in its most basic features, does not substantially change across latitudes. Unlike on land, where primary production and the extent of the three-dimensional space created by the vegetation are generally and directly tied, the floating phytoplankton does not create supporting structures to compete for light. Its vertical distribution is variable in space and time and does not necessarily depend on primary productivity. Although pelagic habitats may flip between different states at a local or even global scale due to alternative climatic equilibria across different timescales, changes in species composition in marine pelagic waters are not as slowly proceeding and persistent as those given by succession in marine benthic or terrestrial environments.

The following paragraphs broadly outline our methods. A more detailed description is provided in appendixes A, C, and D in the online edition of *American Naturalist.*

Methods

To address alpha diversity, we divided the world's coastlines into 642 geographic sectors (fig. 1). The subdivision into oceanographic regions shown in different colors helps to screen whether a pattern is general or conspicuous regional variation exists. A conceptual framework reflects 13 domains of most immediate rationales that are specified in detail in appendix B in the online edition of the *American Naturalist.* It predicts positive or negative effects on species richness for 59 of the 66 parameters that were taken into account (table 1). While the meaning of the parameters representing these rationales is self-explanatory, a more detailed description is provided in appendix C. The set of species regularly foraging in marine pelagic waters during the breeding season (R) includes species also foraging in nonpelagic habitats. More rigid is the subset of species exclusively foraging in marine pelagic waters (E), for which we recalculated parameters that depend on species composition or breeding season. Product-moment correlation coefficients (table 1) refer to log- or (in the case of percentages) arcsine-transformed variables. We distinguish between two classes of energetic parameters acting at the local scale: the local energy supply by the environment (local annual net primary production; parameters 1–3) and the energy actually appropriated by the seabird communities (energy flux and community size: parameters 4, 5). We use the best predictor of species richness in each of these two classes in sets R and E (fig. 2) to explore which parameters have the potential to explain further variation of species richness in the presence of energetic parameters (table 1; details of these models are given in
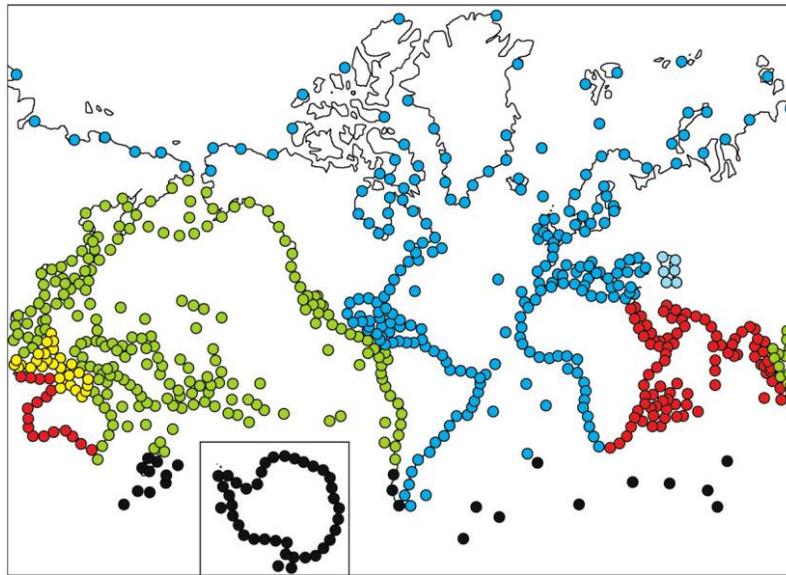

Figure 1: Global partitioning of the world's coastlines defining the data input. Each dot represents one of 642 sectors along continuous coastlines (including the Caspian Sea as a continental saltwater basin), within island groups/chains of about 500-km diameter, or on isolated oceanic islands. Different colors denote geographic sections not strictly corresponding to biogeographic provinces.

Table 1: Potential determinants of seabird species richness (alpha diversity) in the total set of species regularly foraging in marine pelagic waters when breeding (R) and the subset exclusively foraging in these waters when breeding (E)

Parameter	MIR	R				E			
		r	r²	N/df	TPM	r	r²	N/df	TPM
1. Local ANPP, within 125 km	a+, d7+	.37***	.14	642/152	5	.37***	.13	642/248	
2. Within 1,000 km	a+, d7+	.33*	.11	642/127		.47***	.22	642/138	
3. Within 1,000 km (Voronoi)	a+, d7+	.29	.08	642/158		.51***	.26	642/115	
4. Energy appropriation (seabird community)	a+	.52***	.27	630/113	1	.55***	.30	510/140	
5. Community size (breeding pairs)	a+	.54***	.29	630/100	1	.53***	.28	630/159	
6. No. nonbreeding species	a−	−.03	.00	642/77	1	.07	.00	642/80	
7. Mass-specific metabolic rate	b+	.11	.01	630/149		.13	.02	510/95	
8. Global ANPP: within 1° of sector midpoint latitude	c+	.28	.08	642/81	1, 5	.14	.02	642/157	4
9. Within 5° of sector midpoint latitude	c+	.30	.09	642/78	1, 5	.15	.02	642/154	4
10. Within 9° of sector midpoint latitude	c+	.32	.10	642/75	1, 5	.16	.03	642/149	4
11. Global ANPP: SST ± 0.5°C	c+	−.28	.08	642/76		−.06	.00	642/98	
12. SST ± 1.5°C	c+	−.30	.09	642/75		−.08	.01	642/114	
13. SST ± 2.5°C	c+	−.31	.09	642/69		−.08	.01	642/114	
14. Maximum altitude within 50 km	d1+	.27**	.07	642/214	1, 5	.11	.01	642/260	
15. Fractal dimension (continuous coastlines)	d2+	.25	.06	471/103	1	.11	.01	471/114	4
16. No. islands (continuous coastlines)	d2+	.34*	.11	471/99	1, 5	.11	.01	471/113	3
17. Day length (breeding season)	d2±	.13	.02	630/70	1+	−.04	.00	510/143	4−
18. Tidal amplitude	d3+	.05	.00	642/122		.13	.01	642/189	
19. Number of rivers (continuous coastlines)	d3+, m+	.20	.04	471/71	1, 5	−.11	.01	471/86	
20. Minimum shelf width: smallest value	d4±	.14	.02	642/190	1+, 5+	−.29*	.08	642/150	3−, 4−
21. Largest value	d4±	.14	.02	642/155	1+, 5+	−.30	.08	642/124	3−, 4−
22. Maximum shelf extent	d4±	.18	.03	642/142	1+, 5+	−.24	.05	642/122	4−
23. Maximum depth within 125 km	d4±	−.02	.00	642/204		.30**	.09	642/189	3+, 4+
24. Wind speed (breeding season)	d4+	.35*	.12	607/143	1	.26***	.06	483/295	
25. Wave height (breeding season)	d4+	.24	.06	607/115		.45***	.20	483/116	3, 4
26. Local marine pelagic area: within 125 km	d4+	.02	.00	642/243		.36***	.13	642/147	3, 4
27. Within 1,000 km	d4+	.03	.00	642/110		.41*	.16	642/67	3, 4
28. Within 1,000 km (Voronoi)	d4+	.08	.00	642/147		.44***	.20	642/85	4
29. Light intensity during the day	d5+	−.23	.05	642/60		−.08	.01	642/131	4
30. SST (breeding season)	d6+, h+	−.02	.00	630/64	5	−.03	.00	510/212	4
31. Latitude	d6−, h−, k−	.32	.10	642/65		.16	.02	642/119	4
32. Proportion of species foraging offshore	e4+	.12	.01	630/190		.28*	.08	510/178	

Table 1 (*Continued*)

Parameter	MIR	R				E			
		r	r^2	N/df	TPM	r	r^2	N/df	TPM
33. Proportion of under-water foraging species	e5+	.22	.05	630/161	1	.13	.01	510/191	
34. Breeding habitat: niche width	f1−	.15	.02	630/123		.06	.00	509/203	
35. Niche overlap	g1−	−.08	.00	610/186	1	.06	.00	415/149	
36. Breeding season: niche width	f2−	−.27	.07	630/76	1, 5	−.08	.01	510/100	
37. Niche overlap index 1	g2−	−.42***	.17	610/109	5	−.41***	.17	415/142	3
38. Niche overlap index 2	g2−	−.05	.00	610/318	5	−.11	.01	412/210	4
39. Vertical foraging habi-tat: niche width	f5−	−.03	.00	630/178		.11	.01	509/133	
40. Niche overlap index 1	g5−	.11	.01	610/408		−.02	.00	414/288	
41. Niche overlap index 2	g5−	.02	.00	610/200		.09	.01	413/217	
42. Food type prefer-ences: niche width	f6−	.21	.04	630/119		.23	.05	509/156	
43. Niche overlap	g6−	−.32**	.10	607/144		−.27**	.07	411/202	
44. Ambient air tempera-ture at land: all months	h+	.04	.00	642/69		−.06	.00	642/213	4
45. Breeding season	h+	.05	.00	630/95	5	−.00	.00	510/186	4
46. Fecundity	i+, j+	−.00	.00	630/174	5	−.37***	.13	510/187	
47. Body mass	j−, d8+	.10	.01	630/161		.17	.02	510/82	4
48. Global marine pelagic area: within 1° of sec-tor midpoint latitude	k+	−.09	.01	642/58		−.01	.00	642/154	4
49. Within 5° of sector midpoint latitude	k+	−.07	.00	642/60		.01	.00	642/161	4
50. Within 9° of sector midpoint latitude	k+	−.05	.00	642/61		.02	.00	642/166	
51. Global marine pelagic area: SST ± 0.5°C	k+	−.42*	.18	642/58		−.11	.01	642/72	
52. SST ± 1.5°C	k+	−.44*	.20	642/56		−.16	.02	642/83	
53. SST ± 2.5°C	k+	−.44*	.19	642/57		−.16	.02	642/91	
54. Global area: within 1° of sector midpoint latitude	k+	−.07	.00	642/59		.01	.00	642/160	4
55. Within 5° of sector midpoint latitude	k+	−.05	.00	642/60		.01	.00	642/165	4
56. Within 9° of sector midpoint latitude	k+	−.04	.00	642/60		.02	.00	642/167	4
57. Human population density: minimum	l±	−.08	.00	642/122		−.21	.04	642/113	3−
58. Maximum	l±	.03	.00	642/96		−.21	.04	642/111	3−
59. Negative human ef-fects on population size	l−	.14	.02	630/113		.10	.01	510/93	
60. Negative human ef-fects on range size	l−	.25*	.06	630/182		.12	.01	510/97	
61. Positive human ef-fects on population size	l+	.35**	.12	630/113	1, 5	.05	.00	510/155	
62. Positive human ef-fects on range size	l+	.28	.08	630/91	1, 5	.02	.00	510/171	
63. No. lakes (continu-ous coastlines)	m§	.25	.06	471/50	1, 5	−.05	.00	471/58	
64. Humidity at land (continuous coastlines)	m§	.19	.04	471/108	1, 5	−.08	.00	471/75	

Table 1 (*Continued*)

| Parameter | MIR | R | | | | E | | | |
		r	r²	N/df	TPM	r	r²	N/df	TPM
65. Proportion of species not exclusively pelagic	m§	−.03	.00	630/177	5	−.37**	.14	510/100	4
66. Proportion of ranges not exclusively marine	m§	−.05	.00	630/147	5	−.42**	.17	510/98	4

Note: Product-moment correlation coefficients *r* and variation explained *r*² in set R and subset E (species regularly and exclusively foraging, respectively, in marine pelagic waters when breeding); *N* denotes the number of sectors considered; df is the spatially adjusted degrees of freedom. Most immediate rationales (MIR; specified in detail in app. B in the online edition of the *American Naturalist*) and associated predictions (expected sign of the correlations: positive [plus sign]; negative [minus sign]; positive or negative [plus-minus sign]; § = positive for R, negative for E): a, local supply rates of available energy; b, rates of molecular evolution; c, amount of suitable habitat at the global scale limits the ecological saturation at the alpha level; d, geometric and physicochemical complexity of the environment limits the niche space that may be filled by competing species (1 = breeding habitat, 2 = breeding and foraging habitat, 3 = foraging habitat, 4 = on the horizontal gradient from coastal to oceanic waters along which foraging takes place, 5 = along the vertical gradient in the water column along which foraging takes place, 6 = diversity of potential prey, 7 = niche space created by the spatial variability of energy supply, 8 = food-item size and associated trophic level); e, niche space (see d); f, niche width (see d); g, niche overlap (see d); h, immediate impact of cold climates, like those related to the Plio-Pleistocene glaciations; i, number of progeny produced per year defines strength of selection and thereby macroevolutionary adaptability of gene pools; j, correlate of generation time defining rates of molecular evolution; k, likelihood of geographic speciation (isolation by distance); l, anthropogenic impact: reduction or eradication of seabird populations due to direct persecution, introduction of nonindigenous predators, habitat modification/destruction, overfishing or various forms of pollution; increase or expansion of seabird populations due to an augmentation of food accessibility or quality owing to fishing activities or efficient executive conservation authorities in prospering economies; m, potential bias in the data due to species obtaining energy from other than marine pelagic habitats. TPM specifies whether significant two-predictor models (linear backward stepwise regression coefficients matching the prediction of MIR) may exist, which, in combination with parameter 1 and/or 5 (set R) and 3 and/or 4 (subset E) respectively, explain further variation under consideration of scenario II (see "Methods"). ANPP = annual marine pelagic net primary production; SST = sea surface temperature; asterisks indicate scenario I (spatially adjusted) significance.

 * $P < .05$.
 ** $P < .01$.
 *** $P < .001$.

table F1 in the online edition of the *American Naturalist*). The two-parameter models refer to linear backward stepwise regression coefficients and the associated variation explained (Statistica for Windows, release 4.5, StatSoft). Bearing in mind that multiple regression techniques are ambiguous in identifying causality and ranking variables by their importance (James and McCulloch 1990), we kept the study conservative by not adding more than one supplementary variable. Probabilities are Bonferroni-corrected (bivariate associations: *P* level/66; two-predictor models: *P* level/132). We consider two scenarios of spatial autocorrelation that correspond to different epistemological designs, namely, hypothesis testing and associated Type I errors (table 1) and exploratory formulation of hypotheses (TPM in table 1; table F1) for which consideration of Type II errors may be relevant. Both scenarios are explained in detail in appendix D. We applied the program Spatial Analysis in Macroecology (Rangel et al. 2006) to use Dutilleul's (1993) approach to adjust degrees of freedom and probabilities of table 1.

Results

Available Energy and Other Potential Predictors of Species Richness

The best predictors are found among energy-related variables (parameters 1–5; table 1). Significant associations related to other parameters are far weaker than energy appropriation and community size (parameters 4, 5), which potentially account for 27%–30% of the variation in species richness. An index of seasonal niche overlap (parameter 37) is the best nonenergetic predictor; however, this index is likely to be biased due to the scanty knowledge of spatial variation in the phenology of tropical seabirds and the simplistic assumption that the breeding cycle of all species generally covers all months in the tropics, which is obviously not correct (Le Corre 2001). Another index of seasonal niche overlap that avoids this bias by considering breeding cycle length instead of breeding season (parameter 38) is not significant at all. Also, the negative correlation between niche overlap drawn from preferred food types (parameter 43) and species richness match the prediction, but it is the consequence of a spurious correlation that could easily be traced; in unproductive waters, the preferred sort of prey of the great majority of species is a single prey type, namely, fish, while crustaceans and cephalopods become increasingly important components of seabird food as productivity increases (Hashmi 2002). In consequence, niche overlap is inevitably high where the supply of available energy is low, and it produces a negative association between niche breadth and niche overlap (details are described in figs. E1 and E2 in the online edition of the *American Naturalist*) that does not really indicate reduced niche width. Furthermore, extremely productive
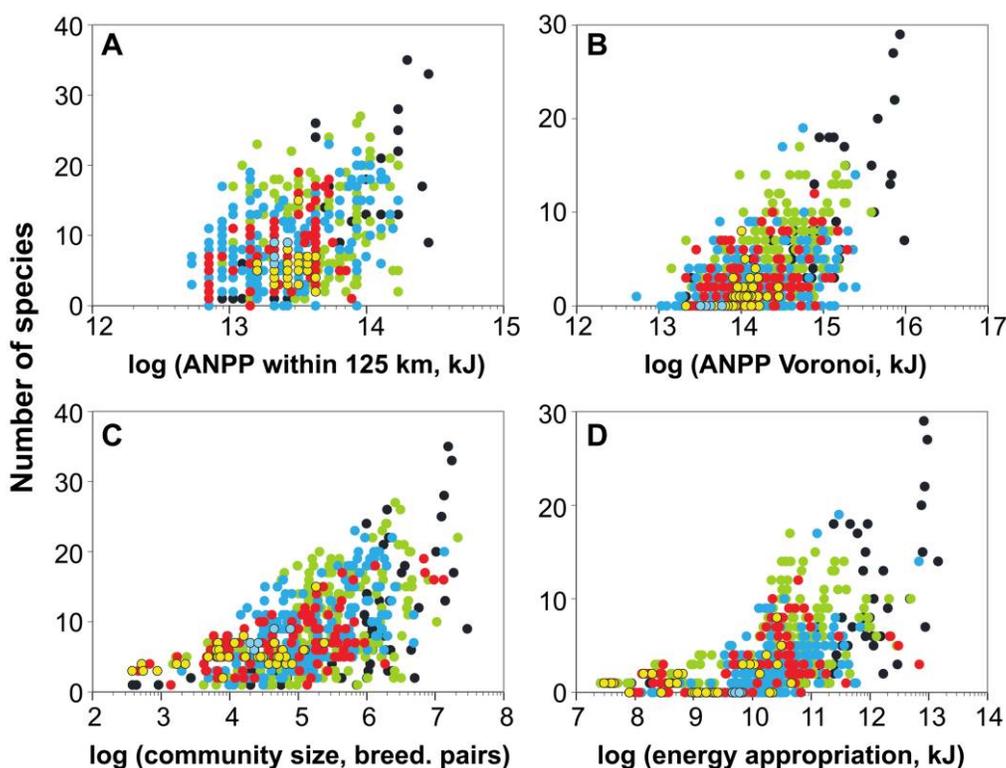
Figure 2: Seabird species richness versus energetic parameters listed in table 1: *A*, parameter 1, set R (birds regularly foraging in marine pelagic waters during the breeding season); *B*, parameter 3, subset E (birds exclusively foraging in marine pelagic waters during the breeding season); *C*, parameter 5, set R; *D*, parameter 4, subset E (see fig. 1 for the meaning of colors).

communities exhibit considerable niche overlap (as specified in figs. E3 and E6 in the online edition of the *American Naturalist*), which henceforth can be excluded as an explanation for high species richness in response to energy supply at the given resolution. At a finer resolution of prey types, the diversity of potential prey could still be relevant. However, as diversity of potential prey is positively correlated with latitude (Macpherson 2002; parameter 31), significant effects of niche space, or combined effects of niche width and overlap, do not comply with the observed relationship between available energy and species richness. One may still argue that even without taxonomic diversity of potential prey, food items of different size within or between different trophic levels might permit specialization along single resource axes (Hutchinson 1959). An increase of seabird body mass (parameter 47) or of its variation with species richness would support this idea, but body mass is not significantly correlated and homoscedastic.

Good predictors of species richness that do not match the sign of the framework (parameters 46, 51–53, 60) are correlates of determinants of species richness but are not

helpful in identifying causation. Of the energy-related parameters, energy appropriation and community size (parameters 4, 5) explain far more variation than local primary production (parameters 1–3), yet both aspects match the idea that available energy constrains maximum species richness, while several other factors prevent most communities from reaching this limit (fig. 2). At large scales, within geographically defined subunits of the system studied, the limitation of species richness by available energy seems to be universal.

Although nonenergetic predictors of species richness matching the framework have far less predictive power than the best energetic determinants, several parameters deserve attention. In species-rich communities, higher proportions of species commute to foraging grounds far away from the coast (parameter 32), which is a consequence of energy supply rather than a response to a change of other physical characteristics of the environment along this gradient. Wind and waves may make vital contributions to this pattern, especially in subset E, and for several reasons that are not mutually exclusive. Wind and waves may (1) facilitate upwelling of nutrients and therefore aug-

ment primary production and, in turn, seabird production. Simultaneously, as nontrophic auxiliary energy sources, wind and waves permit locomotion styles that reduce field metabolic rates (Ballance 1995) and thereby potentially (2) enhance the number of individuals in a community regardless of trophic energy acquisition; longer commuting distances may simultaneously (3) increase the energy appropriation by the community and (4) widen horizontal niche space, which may already be defined by adaptations to commuting distances and extended absence from the nest. Although extension of niche space may augment species richness independent of trophic energy supply (rationale d in table 1), in the system studied, it directly connects to the appropriation of available energy.

Competition between species exclusively and not exclusively foraging in marine pelagic waters (parameters 65, 66) may explain why shelf characteristics (parameter 20), water depth offshore (parameter 23), and local marine pelagic area (parameters 26–28) are significant predictors only in set E.

Potential Codeterminants of Species Richness

We use the best predictors of species richness related to local energy supply as well as energy appropriation to explore whether potential correlates, such as wind and waves, may act as independent determinants of species richness (table 1; for details see app. F in the online edition of the *American Naturalist*). These two-predictor models remain exploratory in nature; hence, we will not elaborate on details. It is obvious that a number of associations, including wind and waves, match the framework and may support or suppress species richness along the gradient given by trophic energy supply. However, the increase in the variation explained is modest if secondary parameters matching the sign of the framework are added to community size (up to factor 1.48, from 29% to 43%; parameter 16) or energy appropriation (up to factor 1.31, from 30% to 37%; parameter 28, 65, or 66).

Discussion

While the two-predictor models underline that a variety of factors are likely to codetermine seabird diversity, the focal point made here is that the energy flux appropriated by the community as a whole can be discriminated from other potentially relevant factors as the major determinant of species richness. It is important to understand that this is not a sampling effect. In species-rich communities, it is often necessary to use species-individual curves to estimate species richness at the alpha level. Here we know with adequate precision the total number of seabird species coexisting at the alpha level. Ecological as well as evolu-

tionary mechanisms may underlie the energetic limitation of the number of species. In this system with pronounced niches, species richness does not automatically increase with the number of individuals but may depend on (1) an energetic determination of competition and associated selective recruitment of species and/or (2) an energetic control of diversification. Although this analysis cannot distinguish between these mechanisms, it pinpoints that the trophic energy flux is relevant per se in this system and may stimulate work that investigates whether energy supply affects speciation and/or extinction rates. Overall, we assume that an energetic control of diversification may be given by opportunities for adaptive radiation. More importantly, the results suggest that this control is determined by the actually realized trophic energy appropriation rather than by primary productivity. Because potential determinants of rates of molecular evolution (parameters 7, 46, and 47) do not systematically vary with trophic energy flux in this system, molecular clocks may help to explore whether in situ diversification by adaptive radiation or ecological recruitment is more decisive.

In other studies, single-parameter models referring to variables that can be related to available energy often explain more than 60% of the variation of species richness (Hawkins et al. 2003). With up to 30%, the predictive power is modest in the seabird system. The reason for this difference may well be that available energy is usually widely congruent with other determinants of species richness, which implies that the correlations in these studies need not be due to available energy as such. In any case, no comparison is possible unless other studies exist in which available energy can be separated from correlated but distinct causation.

This study deals with large-scale patterns of biodiversity that have formed over timescales in which communities had enough time to assemble and evolve, even though it is not known whether an evolutionary equilibrium of species richness had been reached at the alpha level. It does not claim that fertilization or a short-term enhancement of energy supply would necessarily augment seabird diversity. Table 1 suggests that species that are not exclusively pelagic currently benefit from available energy made accessible by the presence of humans (parameter 61). We cannot exclude that such patterns may also apply to exclusively pelagic species, because we had no access to data on the intensity of fisheries at sea. In this context, it should be mentioned that eutrophication or access to discards of commercial fisheries may lead to a replacement of specialized endemics with globally well-represented generalists or even decrease the number of species instead of enhancing it.

The limitation of species richness in seabird communities is markedly different from that in communities of

terrestrial endotherms and communities of marine exotherms. Forest bird communities in the diverse tropics and far less species-rich temperate climates do not necessarily differ in energy flux and abundance (Karr 1971; Terborgh et al. 1990). Variation in geometric and physicochemical complexity of the niche space offered by the environment seems to be far more decisive. This may also be true for seabird communities, however, which marks a very special situation, in that this complexity is not created by the environment but by evolutionary radiation directly represented by the amount of available energy appropriated. Correlations between solar energy and species diversity in temperate songbird communities, especially in winter, may be due to food accessibility and ambient temperature as an auxiliary relief of high metabolic rates related to an endothermic life style (Elkins 1989). In hermatypic coral reefs, solar radiation and temperature may be good predictors of photosynthetic energy fixation (Fraser and Currie 1996), but it remains difficult to separate energy flux as such from other potential determinants. For heterotrophic exotherms, such as lepidoptera (Turner et al. 1987) on the continents or zooplankton (Rutherford et al. 1999) and bivalves (Roy et al. 2000) in the seas, temperature and solar radiation are the best correlates of species richness. An inherently greater number of niches caused by temperature dependence of metabolic rates and the associated macroevolutionary potential to reduce niche width and thereby competition (Vermeij 1978) are among the most straightforward explanations for the redundancy of exothermic species in warm waters. Simultaneously, rates of molecular evolution may be higher as a consequence of mass-specific metabolic rates or of solar radiation in transparent organisms. Highly productive pelagic waters are comparatively cold, at high latitudes as well as in the tropics. Restricted thermal mutagenic effects and glacial extinctions are among the most attractive ideas why marine exotherms are often not diverse in productive waters. Therefore, one important implication of this study is that large-scale gradients of biodiversity, such as the latitudinal increase of species richness from the poles to the equator, are the consequence of a number of constraints that may strongly vary across different taxa, guilds, regions, and periods. On average, these usually bring about higher species richness in the tropics. Although energy supply is of cardinal importance for the ultimate limitation of biodiversity if other restrictions are negligible, as validated by the seabird system, a single mechanism that explains this gradient does not exist, and it is often impossible to infer causation from given patterns. Seabird communities constitute a comparatively simple situation of a distinct guild that has secondarily spread into marine pelagic waters while displaying diversification and adaptive radiation of birds. Even in this relatively lucid system, it may be difficult

and ambiguous to single out determinants of species richness beyond energy supply, for which a quasi-experimental design is broadly met.

Acknowledgments

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