Supplementary Materials

Measuring Cumulative Diversity and Its Components

Table S1. Diversity measures used in Whittaker partition and the new hierarchical partition with measures from Tuomisto [26,27]. Formulae presented for diversity of order 2 (i.e., q = 2). Symbols & subscripts: p_i = relative (proportional) abundance of species i in local community (i.e., $\mathbf{N_i}/\sum \mathbf{N_i}$); p_j = proportional abundance of organisms occurring at time j (i.e., $\mathbf{N_j}/\sum \mathbf{N_j}$); D_j = diversity as number of effective species in local community at time j; S_j = species richness of local community at time j.

Diversity Measure	Symbol	Formula	Description	Reference
Gamma diversity	γ_D	$\mathbf{1/\sum_{i}^{S} p_i^2}$	*Cumulative diversity:* Long-term diversity of time-aggregated abundance data	Equation (2) in [26]
Gamma richness	γ_S	S	*Cumulative richness:* Long-term richness of time aggregated data	[26]
Gamma evenness	γ_E	$\boldsymbol{\gamma_D/\gamma_S}$	*Cumulative evenness:* Long-term evenness of time aggregated data	[27]
Alpha diversity	α_D	$\mathbf{\sum_{j}^{N} p_j D_j}$	Average diversity of a local community	Equation (33) in [27]
Beta diversity	β_D	$\boldsymbol{\gamma_D/\alpha_D}$	Temporal turnover of diversity	Equation (32) in [27]
Alpha richness	α_S	$\mathbf{\frac{1}{N}\sum_{j}^{N} S_j}$	Average richness of a local community	Equation (10) in [26]
Beta richness	β_S	$\boldsymbol{\gamma_S/\alpha_S}$	Temporal turnover of richness or community composition	Equation (11) in [26]
Alpha evenness	α_E	$\boldsymbol{\alpha_D/\alpha_S}$	Average evenness of a local community	Table 3 in [27]
Beta evenness	B_E	$\boldsymbol{\gamma_E/\alpha_E}$	Temporal turnover of evenness or dominance in local community	Equation (34) in [27]

Null Expectations of a Local Abundance–Diversity Relationship

Diversity and richness often increase by the addition of low abundance species to a stable core of abundant species [2,18,19]. This metacommunity dynamic implies that the abundance of the average community member will decrease as species (or effective species) are added. Here we confirm this diagnostic pattern—a negative abundance-diversity relationship—with simple simulations.

We simulated the addition of progressively rarer species to a community, up to the maximum richness seen in a single rock pool (29 species). We drew the mean abundance of a species from a lognormal distribution and added noise from a uniform distribution to its time series (t = 14 time steps). To generate abundance–diversity relationships, we added species in rank order from most to least abundant. Figure S1a shows that adding progressively rarer species to a community increases cumulative diversity while decreasing mean local abundance, resulting in the predicted negative relationship. The same averaging phenomenon produced a negative local abundance–richness relationship (Figure S1b) in which newly-added rare species pull down the average abundance of species in the local community. A positive relationship between mean abundance and cumulative evenness also emerged (Figure S1c) reflecting that adding rare species simultaneously lowers mean abundance and community evenness.

Distinctly different patterns are produced if progressively more abundant species are added to the community. In this case, a parabolic abundance–diversity relationship emerged (Figure S2a) as diversity initially increases by the addition of slightly more abundant species and then rapidly declines when the addition of hyper-abundant species lowers the number of effective species. Moreover, the abundance–richness relationship is now positive (Figure 2b) because adding abundant species increases the average abundance and species count. Lastly, the abundance-evenness relationship becomes negative (Figure 2c) as the addition of abundant species inflates average abundance and reduces evenness.

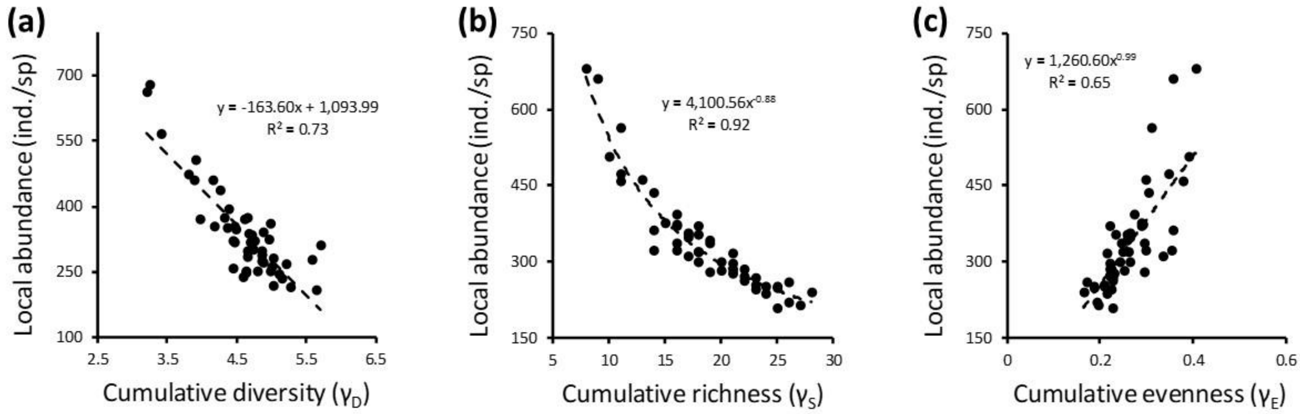

Figure S1. Simulated relationships between mean local abundance of species and (**a**) cumulative diversity, (**b**) cumulative richness and (**c**) cumulative evenness when species accumulate in order from high to low abundance.

Adding species in random order of abundance eliminated abundance–diversity and –richness relationships (Figure 3a,b), but not the abundance–evenness relationship (Figure 3c). This may be because the presence of rare species will always tend to reduce average abundance and evenness, regardless of the order in which they are added to the community.

Simulations confirm that negative abundance–diversity and –richness relationships are indicative of a well-known metacommunity dynamic in which diversity increases through the accumulation of rare species. The abundance–evenness relationship, in contrast, is a poor diagnostic because it can be produced by statistical happenstance in random community assembly. We also admit alternative explanations for negative abundance–diversity and –richness relationships; for example, if greater species packing and resource competition results in smaller populations of each species as is assumed in classical theory [57] and may occur in natural communities [34]. More common expectations, however, are hump-shaped or positive abundance–diversity relationships driven by underlying relationships between diversity and ecosystem productivity, or no relationship at all [35]. However, since these relationships would be unimodal or positive linear, they would not be confused with the negative linear slopes produced when diversity grows by the addition of rare species.

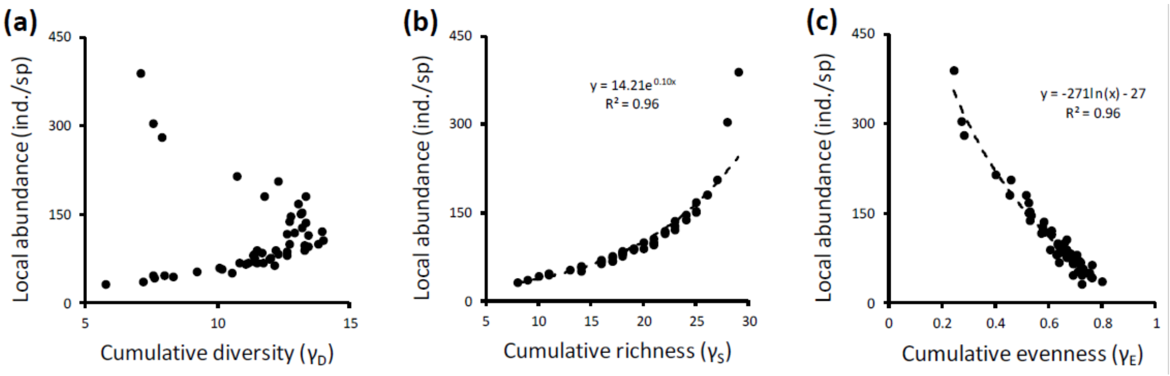

Figure S2. Simulated relationships between mean local abundance of species and (**a**) cumulative diversity, (**b**) cumulative richness and (**c**) cumulative evenness when species accumulate from low to high abundance.

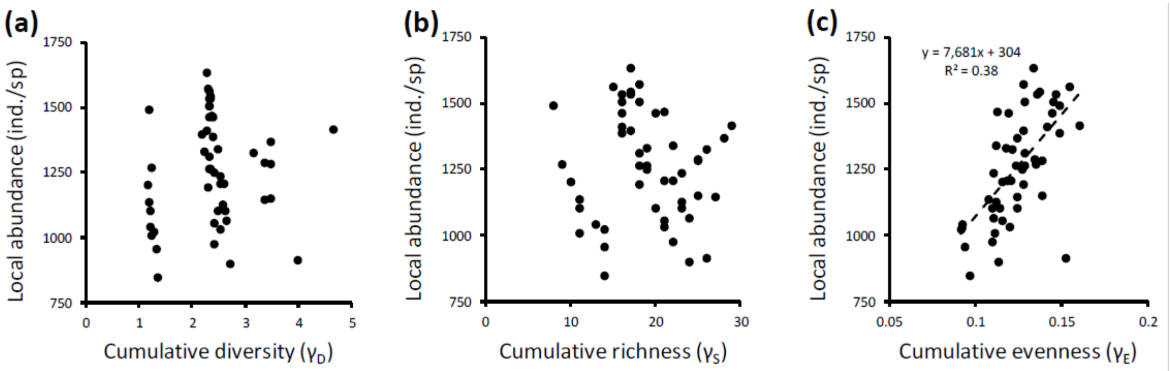

Figure S3. Simulated relationships between mean local abundance of species and (**a**) cumulative diversity, (**b**) cumulative richness and (**c**) cumulative evenness when species accumulate in random order of abundance.

Multiple Regression Results

Table S2. Results of multiple regression models predicting diversity measures from Whittaker's partition (Equation 3) as a function of environmental PCA axes (Physicochemical variation, EV 1 and pool drying, EV 2), mean habitat specialization and mean local abundance against. Significant slope coefficients are bolded.

Response Variable	EV 1	EV 2	Habitat Specialization	Mean Abundance	Intercept	R^2	$F_{3,45}$	*p*
†γ_D	**−0.10*****	**−0.03***	0.54	**−0.00***	0.36	0.59	15.52	<0.0001
*α	**−0.09*****	−0.03	0.77	−0.00	1.19	0.52	11.71	<0.0001
β	**−0.13****	−0.04	0.20	−0.00	1.65	0.29	4.48	0.004

† Log_{10} transformed.* Square-root transformed.

Table S3. Results of multiple regression models predicting diversity measures from a new hierarchical partition (Equation 3) as a function of environmental PCA axes (Physicochemical variation, EV 1 and pool drying, EV 2), mean habitat specialization and mean local abundance. Significant slope coefficients are bolded.

Response Variable	EV 1	EV 2	Habitat Specialization	Mean Abundance	Intercept	R^2	$F_{4,44}$	*p*
†γ_D	**−0.10*****	**−0.03***	0.54	**−0.00***	0.36	0.59	15.52	<0.0001
*γ_S	**−0.08***	**−0.18*****	**9.43*****	**−0.00***	2.41	0.77	36.28	<0.0001
γ_E	**−0.03*****	−0.00	**−0.47***	−0.00	0.27	0.45	8.97	<0.0001
α_S	**−0.66*****	**−0.70*****	**20.84*****	−0.00	1.85	0.61	17.20	<0.0001
†β_S	**0.04****	**0.02***	0.19	−0.00	0.47	0.33	5.43	0.001
α_E	0.00	**0.03****	**−0.97****	0.00	0.52	0.39	7.00	0.0002

β_E	**−0.08*** **	**−0.04***	−0.33	−0.00	0.62	0.45	9.11	<0.0001

† Log_{10} transformed, * Square-root transformed.

Table S4. Results of multiple regression predicting mean habitat specialization as a function of mean salinity and salinity range of a pool. Significant slope coefficients are bolded.

Response variable	Mean salinity	Salinity range	Intercept	R^2	$F_{2,46}$	p
*Habitat specialization	**0.58****	**−0.54****	0.45	0.20	5.78	<0.0001

* Square-root transformed.

Compensatory Effects Within and Among Pathways to Cumulative Diversity

Several compensations were detected in which a factor reduced one component of cumulative diversity but increased another. Figure S4 plots two compensations that existed with the richness and evenness paths to cumulative diversity. In Figure S4a, physicochemical variation reduced the average richness of communities but increased compositional turnover. We estimated the power of this compensation by comparing the impact (slope) of EV on average richness with its impact (slope) on cumulative richness. This quantity measures how much less impacted—or buffered—cumulative diversity is by EV than its most severely impacted component. Expressed as a percentage, EV 1 affected cumulative diversity 67% less than it did its alpha diversity component. Figure S4b, meanwhile, shows the positive effect of pool drying on average evenness compensated by a decline in evenness turnover. This compensation effectively buffered cumulative evenness by 125%.

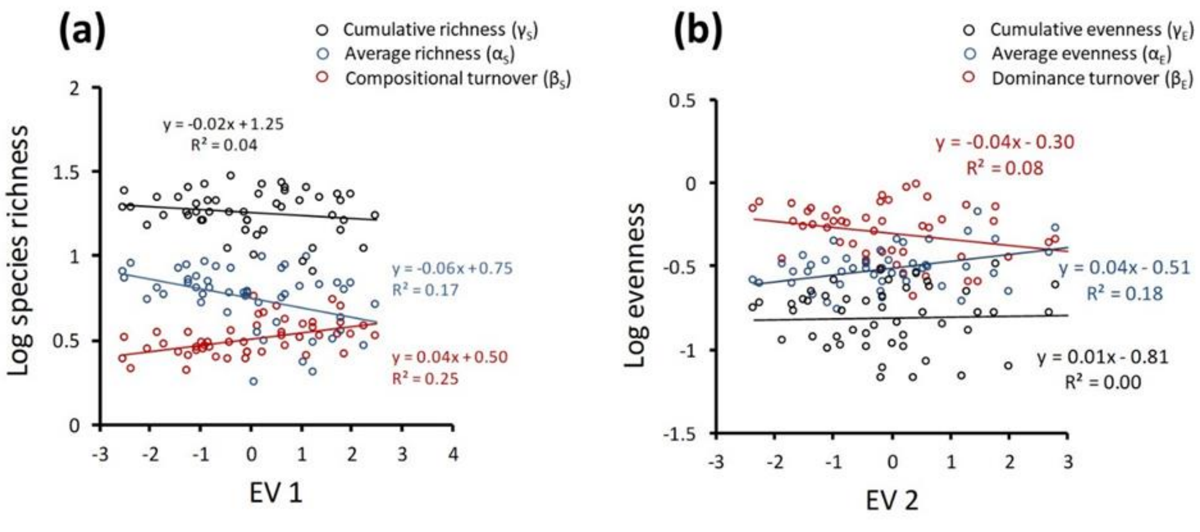

Figure S4. Opposing effects of environmental variation on components (**a**) within the richness path and (**b**) within the evenness path that cancel out and buffer impacts at higher hierarchical levels (on cumulative richness and cumulative evenness, respectively).

Compensations also occurred among pathways. Figure S5 illustrates the opposing effects of habitat specialization on cumulative richness and evenness, which cancel out and reduce the impact of the factor on cumulative diversity. We estimated the magnitude of this stabilizing effect to be 65%.

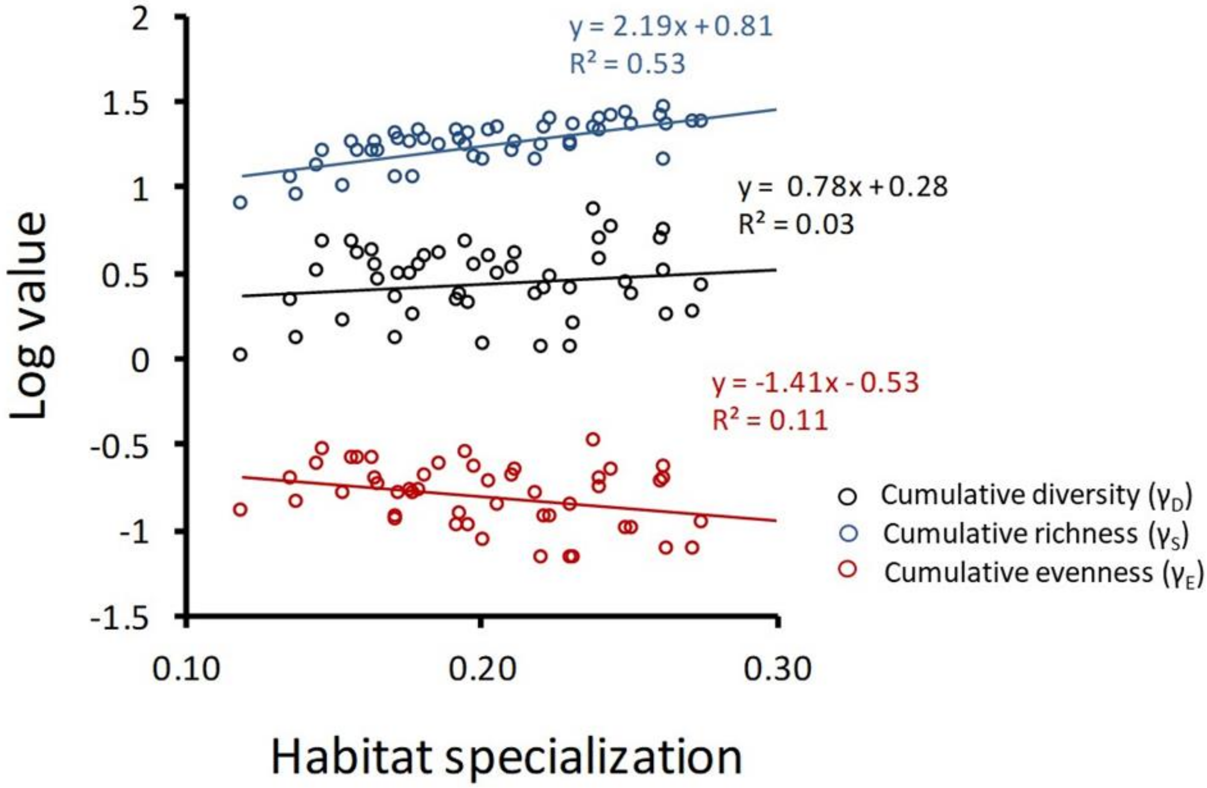

Figure S5. Opposing effects of environmental variation on cumulative richness and cumulative evenness that cancel out and buffer environmental impacts on cumulative diversity.