ÉCOSCIENCE 8 (2) :259-263 (2001)

# Simplifying the complexity of temporal diversity dynamics: A differentiation approach[1]

Tamara N. ROMANUK[2] & Jurek KOLASA, Department of Biology, 1280 Main Street West, McMaster University, Hamilton, Ontario L8S 4K1, Canada, e-mail: romanutn@mcmaster.ca

*Abstract*: **A** simple, yet highly promising method of quantifying temporal diversity dynamics is to use the ratio of mean species richness, **S,** to potential species richness, **P** (cumulative S at a locality). In a **rock** pool meta-community of aquatic micro-invertebrates, this ratio, which **we** call the dynamics index (I), proved reliable as a predictor of assemblage type. We calculated within-habitat diversity dynamics for each of 49 pools that differed in environmental variability. The resulting dynamics indices provide an easily quantified measure of the diversity dynamics at various scales and, specifically, provide a measure of within-habitat temporal turnover in habitats where **P** can he reliably evaluated.
***Keywords:*** species richness, diversity, beta diversity, habitat variability, dynamics index, aquatic, invertebrates, tropical rock pools.

*Résumé* : Une méthode simple mais très prometteuse de quantifier la dynamique temporelle de la diversitt est d'utiliser le rapport entre la moyenne de la richesse spécifique, **S, pour** des échantillons prélevés à différents moments, dans un lieu donné, et la richesse spécifique potentielle, **P** (richesse spécifique cumulative). Pour les micro-invertébrés aquatiques occupant une série de cuvettes rocheuses, ce rapport, que nous appelons indice de dynamique (I), s'est montré fiable comme outil permettant de prédire le type d'assemblage. Nous avons calcult I **pour** chacune de 49 cuvettes rocheuses difftrant quant a leur variabilité environnementale. Les indices calculés foumissent une mesure rapide de la dynamique de la diversitt à difftrentes échelles et, plus particulièrement, une mesure du renouvellement temporel des espèces pour les habitats où **P** peut être estimé de façon fiable.
*Mots-clés* : cuvettes rocheuses en milieu tropical, diversitt, diversitt beta, indice de dynamique, invertébrés aquatiques, richesse spécifique, variabilité environnementale.

## Introduction

Whittaker (1972) suggested two categories, inventory diversity and differentiation diversity, as a framework for describing diversity dynamics. Alpha diversity, or species richness, **S,** is the local diversity of an area and is a component of inventory diversity, **i.e.,** the number of species within a site at various spatial scales (alpha, gamma, epsilon diversity). Beta diversity, or differentiation diversity, is either the turnover of species between localities (the spatial component) or within a locality (the temporal component). While it is difficult to identify these spatial and temporal measures of diversity in a strict operational sense (Loreau, 2000), they are related to each other in either a nested (inventory diversity) or operational fashion (differentiation diversity). Furthermore, the relationship between the various scales *(i.e.,* local *versus* regional diversity) has been shown to be amenable to analysis in convenient settings (Ricklefs, 1987; Cornell & Lawton, 1992; Cornell & Karlson, 1997; Srivastava, 1999).

While differentiation diversity or beta diversity has received considerable attention between habitats (see Schluter & Ricklefs, 1993 for review), the temporal differentiation (as distinct from species turnover) within a habitat has received far less attention. Here we present a new diversity index, the dynamics index, which uses differences in either mean ($S_m$) or recorded values of species richness ($S_t$) along with the potential richness of a site (P. cumulative number of species over time) to quantify temporal changes in diversity. We define temporal diversity dynamics in two ways. Mean species richness over time **(S,)** provides a measure of the temporal trend in diversity dynamics, while species richness observed at one time **(S,)** can be used to compare diversity dynamics from year to year. Specifically, $S_m$:P is the ratio of mean species richness on a number of separate occasions ($S_m$) to potential diversity (P), the total (cumulative) number of species recorded in a habitat over time, or $S_t$:P is the ratio of actual species richness at time t ($S_t$) to potential diversity (P). Both $S_m$ and $S_t$ can be used with P diversity to provide the **S:P** ratio. The S:P ratio results in a within-habitat turnover term, which we call the dynamics index **(I)** which ranges from 0.0 – 1.0. I = 1 indicates maximum temporal similarity in diversity, *i.e.,* all species that have been present at that locality over time (P) are also present at a sampling date under analysis ($S_t$), or are always (when **S„** mean species richness, is used) present at that locality, whereas I = 0 indicates maximum temporal dissimilarity.

The dynamics index characterizes the difference between either the mean number of species **(S,)** that are present at a locality, or the species richness **(S,)** observed on one sampling occasion, and the total number of species that can colonize a habitat, *i.e.,* "the potential richness". Thus, potential richness is analogous to a regional species pool (Ricklefs, 1987; Cornell & Lawton, 1992; Cornell, 1993; Cornell & Karlson, 1997) where **S** is plotted as the number of species in a sample or locality as a function of the number of species in a regional species pool. The difference between the dynamics index and the relationship between local and regional diversity lies in the measurement of P as

[1] Rec. 2000.10-10; acc. 2001-03-02.
[2] Author for correspondence.

the cumulative number of species at a site. This differs from regional diversity, which is measured as the cumulative number of species in the "regional" pool, regardless of whether or not that species was ever recorded at the site or whether it even has a potential of occurring there. Thus, for the dynamics method, all members of the pool have occurred in the locality at one or more times. One limitation of P is that it is scale-dependent within a range of measurements. Specifically, P will continue to change until all species regionally available and capable of persisting in a habitat are recorded. This will depend on a number of factors including species dispersal, duration of successional cycle, and habitat variability. We believe that 10 years of observations is sufficient to approximate P in a 50-pool meta-community of invertebrates with a typical generation time of several days and restricted to an area of less than 50 m in diameter. P could be further affected by invasions by new species into the region and by speciation. Neither of these phenomena has been detected in our model system.

The dynamics index values can range from 0.0 to 1.0 (Table I). A low dynamics value indicates that while many species can potentially colonize or have at one time colonized a habitat, few coexist at any one time. If the mean richness over time is used ($S_m$), then a low dynamics score indicates that biotic interactions may have strong controlling effects, and/or that priority effects may be a primary determinant of the type of assemblage encountered at any one time. If the observed richness is used ($S_t$) in the S:P ratio, a low dynamics score may indicate that while many species are potential colonizers, abiotic conditions or strong biotic controls may limit the number of species. It is not unreasonable to suspect that a low dynamics score may indicate strong competition for resources and/or predation. A high dynamics score may indicate an assemblage with few potential colonizers (due to highly variable or extreme abiotic conditions) that selects for a number of highly vagile or tolerant species that are capable of colonizing newly available habitat (such as when a pool fills with water after a dry phase). Conversely, a high dynamics score may also indicate a highly suitable, low variability habitat with no strong resource limitation. conditions in these habitats may be stable, enabling a wide range of species to colonize and persist.

Plotting mean richness ($S_m$) on potential richness (P) is a simple method of characterizing diversity dynamics. This method can be used to plot communities on a **S:P** scatterplot where values of **S** and P, along with their associated variance, can provide a snapshot of assemblage type (Figure 1). A number of hypothetical examples of the "position" of different ecosystems are shown in the S:P scatterplot in Figure 1. Low values in the dynamics index indicate high turnover, or temporal dissimilarity, while high values in the dynamics index indicate smaller changes in species composition within a habitat. A measure of caution should be used when interpreting S:P values over a wide range of community types. Different temporal and spatial scales will impact the resulting ratio. Furthermore, S:P values may shift during succession or during disturbances, necessitating a thorough description of the successional stage/disturbance regime of the community when attempting to use the index to compare broad community types.

## Material and methods

### STUDY SITE AND SAMPLING PROCEDURE

The community we used to illustrate and test the performance of the dynamics index consisted of a micro-invertebrate meta-community inhabiting coastal **rock** pools. The rock pools are formed primarily by rain erosion and are located on a fossil reef on the northern coast of Jamaica, West Indies, at the Discovery Bay Marine Laboratory. The pools are small in size, ranging from 13-215 $cm^2$, and vary from a few centimeters in depth to no more than 37 cm. On average, the pools are located within 1 m of the nearest neighbor and none is separated by more than 5 m from the

**TABLE** I. General characteristics of dynamics index along with the associated species richness values (in parentheses). The range of **S:P** ratio is given as **I.** Note that the **S:P** ratio (I) overlaps across a few values of **S** ***versus*** potential richness. Extreme ecological "types" are presented **to** illustrate the types of assemblages and the structuring controls that may produce different **S:P** ratios. Note that the thresholds for different levels of species richness ***(ie.,*** low, moderate, high) are not quantitatively determined and depend on the system of study.

| | P, Potential Richness | | |
|---|---|---|---|
| **S,** Species Richness | Low (1-3) | Moderate (4-7) | High (8-10) |
| S:P | I : 0.3 - 1.0 | I : 0.14 - 0.42 | I : 0.1 - 0.375 |
| Low (1-3) | Low biotic variability. Extreme environmental conditions. Species selected for variable conditions, high tolerance levels. Often very high abundance (*i.e.,* salt marshes) or very low abundance (highly degraded habitats, pollution, habitat loss). Also characterizes some temporal boreal forests. | Moderate biotic variability. Species may be subject to moderate to strong competition or predation. Priority effects may begin to be seen. | **High** biotic variability. Many potential colonizers but at any one time only a few may be present. Very strong competition for space and resources or high levels of competition. Very strong priority effects may be seen. |
| S:P | | I : 0.57 - 1.0. | **I** : 0.4 - 0.87 |
| Moderate (4-7) | | Little to no biotic variability at **a** moderate level of diversity. Low levels of competition. Symbioses, mutualisms and parasites possible. | Moderate biotic variability but priority effects present. Limited niches present. Competition may play a role. |
| S:P | | | I : 0.8 - 1.0 |
| High (8-10) | | | Little biotic variability in a diverse community. No priority effects. No competition for resources. |

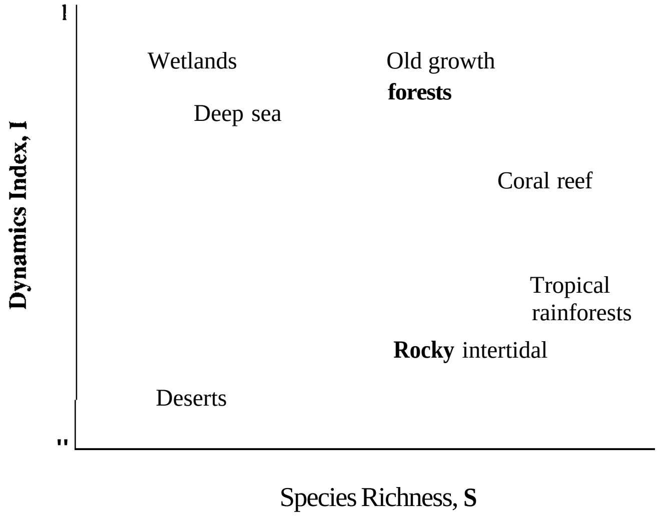


FIGURE 1. Hypothetical relationship between mean species richness (S,) and the dynamics index (I) for different ecosystems. Note that the positions of ecosystems on this **figure** are not static and will be affected by the temporal scale of P used in the index and the successional stage of the ecosystem.

next nearest pool. Their elevation above sea level varies from 0-235 cm at high tide, with the tide rarely exceeding 30 cm. Some pools approach being true tide pools (*n* = 4, tidal flooding is not daily) but most are maintained by atmospheric precipitation and occasional wave splash water.

We sampled 49 pools arbitrarily selected within a radius of less than 50 m (Kolasa *et al.,* 1996). Physical measurements (oxygen, pH, salinity, temperature) were taken on many occasions between December 1989 and June 1997 and averaged for each of the seven dates when communities were sampled. The pools exhibit strong gradients in physical conditions and variability (Schuh & Diesel, 1995). While the pools represent a range of ecological conditions, they contain many species able to colonize and persist in all pools. The pools have significantly different patterns of abiotic variability both diurnally and inter-annually and we use these patterns of variability to assess the performance of the dynamics index. The meta-community is partitioned into freshwater, brackish and marine pools. Freshwater pools are characterized by low inter-annual and low diurnal (24 hour) variability. The marine pools have intermediate diurnal variability and the highest inter-annual variability. The brackish pools are the most temporally variable at diurnal scales and have intermediate inter-annual variability. Overall, 343 samples have been analyzed from 49 pools over seven dates. Sixty-nine species have been identified and counted totaling 226 224 individuals from all samples. These species belong to a variety of freshwater and marine taxa. The full list of the taxa includes: Turbellaria (7), Nematoda (l), Polychaeta (5), Oligochaeta (2), Ostracoda (20), Cope-poda (6), Cladocera (4), Decapoda larvae (4: crab 1 and shrimp 3), Amphipoda (1), Isopoda (1) and Insecta (18). Most species are small benthic animals ranging from 0.5-5 mm but some are plankton-like and swim in the water column.

Species richness **(S)** was calculated as the mean species richness **(S,)** of a pool over seven sampling dates. Potential diversity (P) was calculated as the total number of species found in a pool over all dates. P values can be expected to depend on the length of the period used to obtain cumulative **S,** similar to the dependence of regional **S** on the size of the area chosen for sampling. The length of period we use (10 years) assumes that there is no significant increase in P-values and that species-time curves level off; however, this is not required when the intended use of the index is to compare communities of one meta-community. For inter-system comparisons, reliable assessment of P is critical (see Introduction). The dynamics index was calculated as I = **S,:** P where **S,** is mean species richness and P is potential richness.

## Results

Freshwater pools had the highest **S** (Figure 2a) and an intermediate range P (Figure 2b) indicative of mid-late successional assemblages with low species dispersal (Figure 2a,b). P in the freshwater habitat was intermediate compared to the marine and brackish pools, with a lower limit matching that of the marine pools (Figure 2b). There was a large range in both P and **S** for freshwater pools; however, most (25-75%) of the freshwater pools clustered at a narrow range of richness. The dynamics index (I) of the freshwater pools was the highest of the three habitats, characteristic of the stable diurnal and inter-annual environmental variability regime in these pools (Figure 2c). Freshwater pools are also the highest elevation and deepest pools.

The marine pools had an intermediate **S,** with the range in **S** the highest of the habitats (Figure 2a). There was also a wide range in the 25%-75% percentile for **S** in this habitat type. The marine pools are characteristic of an intermediate disturbance community with a higher inter-annual variability but intermediate diurnal variability. Marine pools also had the largest P range (Figure 2b). The dynamics index (I) for the marine community was the lowest of the three habitat types, indicating a high level of inter-annual temporal dissimilarity of species diversity in a pool (Figure 2c).

The brackish pools had the lowest **S** and the lowest variance of **S** (Figure 2a). P in the brackish pools was low as was the range, with an upper limit matching that of the freshwater pools (Figure 2b). The lower limit of P was higher than for freshwater pools. The brackish habitat had an intermediate I with the highest range in I of all the habitats (Figure 2c).

**A** strong relationship was found between **S** and the dynamics index (I; $r^2 = 0.562$, $P > 0.0001$), however no significant relationship was found between the dynamics index and potential diversity ($r^2 = 0.106$, $P = 0.467$). This latter observation is important, as the dynamics index should be scale independent, ***i.e.,*** independent of the realized pool (potential richness, P) of species. **A** strong correlation was expected for **S** and I as the dynamics index is simply the ratio of S:P. However, it is not the correlation which is of interest, but how the pool communities arrange themselves on the S:P scatterplot (Figure 3). The marine pools show the largest overall variability covering more of the scatterplot than either the freshwater or the brackish habitats. The freshwater pools also cover a significant proportion of the scatterplot but at a lower P range than the marine pools. The brackish pools cover the smallest portion of the scatterplot.

## Discussion

The dynamics index, like turnover or beta diversity (Whittaker, 1972), can be thought of as an average property of species in a region (Schluter & Ricklefs, 1993). Thus, the dynamics index, like beta diversity, can be used in combination with information on vagility to identify taxa (and assemblages) that are more prone to extinction (Haydon, Radtkey & Pianka, 1993). Habitats with a high $S_m$ and a high I are often characterized by assemblages with low vagility and are generally stable. Conversely, habitats with low S, and low I are composed of high vagility assemblages (Isawa *et al.,* 1993) or habitats that have been degraded, subject to rapid environmental changes, or are subject to strong perturbations. It is not unreasonable to expect that

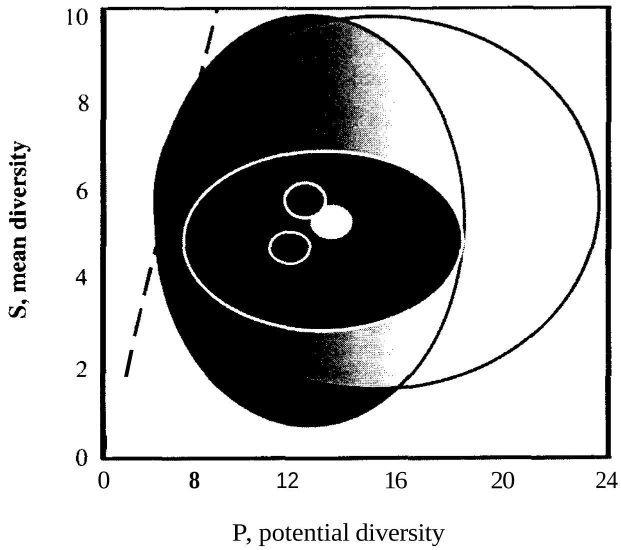


FIGURE 3. Assemblages plotted on the **S** : P scatterplot along with their associated ranges. The small circles denote the median value and the large circles enclose the range for **both** S and **P** in dynamics space. The freshwater assemblage is shaded, the brackish assemblage is black and the marine assemblage is white. The boundary condition (where **S** = P) is shown by the broken line.

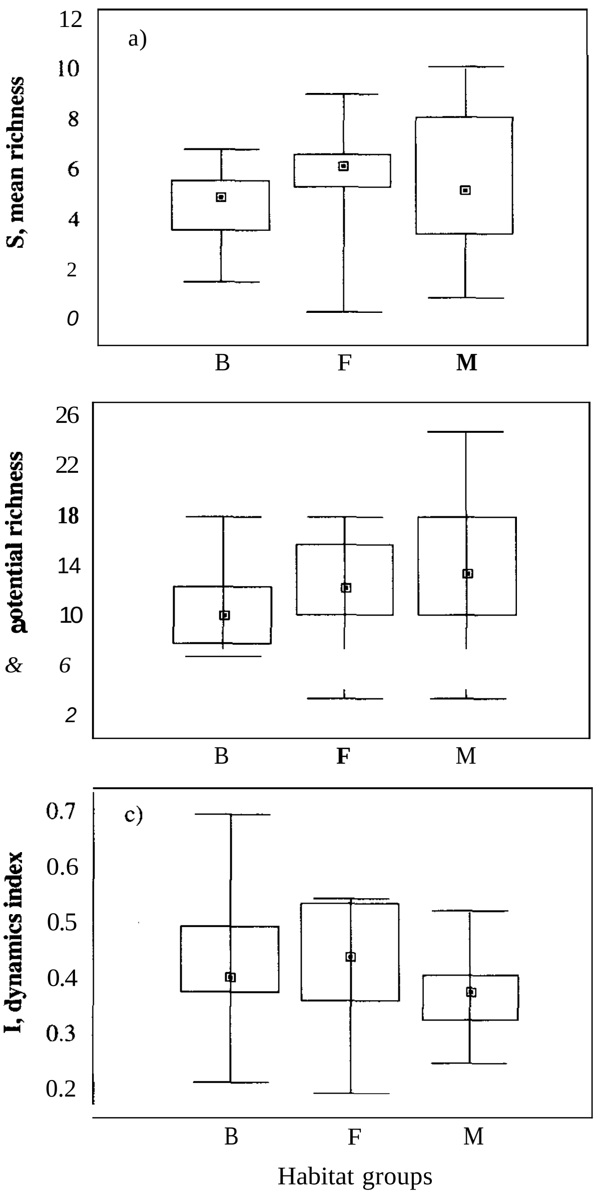


FIGURE 2. a) **S,,** mean diversity, b) **P,** potential (cumulative) diversity and c) I, dynamics diversity **(S:P)** for brackish **(B),** freshwater (F) and marine (M) assemblages. Shown are the range of values, the range of ***25-75%*** values, and the median value.

habitats with high **S,** and low I are communities that experience intermediate levels of disturbance. Habitats with low S, and high I may be occupied by a few, sometimes very abundant, species such as in wetlands or extreme habitats that are dominated by a few highly tolerant species (Figure 1).

In addition to basic characterization of sites according to $S_m$:P and $S_t$:P, a full exploration of the temporal diversity dynamics of a system can incorporate a number of additional derived dynamics metrics. For instance, the variance in $S_t$:P (or standard error in $S_m$:P) can be used to compare sites of different types (i.e., disturbed/undisturbed) or at different successional states. Analyzing the patterns of differences between $S_m$:P and $S_t$:P along habitat clines could also be used to gain additional insights as to the nature of processes affecting diversity.

### USES OF THE DYNAMICS INDEX

We suggest that the dynamics index can be used as a simple method to characterize assemblage type. We envision its use primarily in conservation ecology where basic information on species richness over time can be plotted on the S:P scatterplot to provide a snapshot of assemblage type. The assemblage type in turn can be related to prevailing species attributes such as vagility, extinction probability, tolerance levels, reproductive mode, and others (Isawa *et al.,* 1993). Because a high **S** and low P on the dynamics index is characteristic of a stable yet diverse system (and a low **S** high P is characteristic of a species-poor unstable habitat), the dynamics index may also provide a simple method to identify habitats that are more suitable for conservation and restoration effort.

## Acknowledgements

This research has been supported by an NSERC grant to J. Kolasa. **We** wish to acknowledge the assistance **of T.** Therriault and numerous undergraduates students who contribued to the long-term data set as well as the staff of the Discovery Bay Marine Laboratory, University of the West Indies. J. H. Brown and an anonymous reviewer provided helpful comments and criticisms.

## Literature cited

Cornell, H. V., 1993. Unsaturated patterns in species assemblages: The role of local and regional processes in setting local species richness. Pages 243-252 ***in*** R. **E.** Ricklefs & D. Schluter (ed.) Species Diversity in Ecological Communities. University of Chicago Press, Chicago, Illinois.

Cornell, H. V. & J. H. Lawton, 1992. Species interactions, local and regional processes, and limits to species richness of ecological communities: A theoretical perspective. Journal of Animal Ecology, 61:1-12.

Cornell, H. V. & R. H. Karlson, 1997. Local and regional processes as controls of species richness. Pages 250-268 ***in*** D. Tilman & P. Kareiva (ed.) Spatial Ecology: The Role of Space ***in*** Population Dynamics and Population Interactions. Princeton University Press, Princeton, New Jersey.

Haydon, D., R. R. Radtkey & E. R. Pianka, 1993. Experimental Biogeography: Interactions between stochastic, historical and ecological processes in a model archipelago. Pages 117-130 ***in*** R. E. Ricklefs & D. Schluter (ed.) Species Diversity in Ecological Communities. University of Chicago Press, Chicago, Illinois.

Isawa, Y., K. Sato, **M.** Kakita & T. Kubo, 1993. Modelling biodiversity: Latitudinal gradient of forest species diversity. Pages 433-451 ***in*** E. D. Schulze & H. A. Mooney (ed.) Biodiversity and Ecosystem Function. Springer-Verlag. Berlin.

Kolasa, J., J. A. Drake, G. R. Huxel & C. L. Hewitt, 1996. Hierarchy underlies patterns of variability in species inhabiting natural microcosms. Oikos, 77: 259-266.

Loreau, M., 2000. Are communities saturated? On the relationship between $\alpha$, $\beta$ and $\gamma$ diversity. Ecology Letters, **3:** 73-76.

Ricklefs, R. E., 1987. Community diversity: Relative roles of local and regional processes. Science, 233: 167-171.

Schluter, D. & R. E. Ricklefs, 1993. Convergence and the regional component of species diversity. Pages 230-242 ***in*** R. E. Ricklefs & D. Schluter (ed.) Species Diversity in Ecological Communities. University of Chicago Press, Chicago, Illinois.

Schuh, M. & R. Diesel, 1995. Breeding in a rock pool: Larvae of the semiterrestrial crab *Armases* **[ =** ***Sesarma*****]** ***miersii*** (Rathbun) (Decapoda: Grapsidae) develop in a highly variable environment. Journal of Experimental Marine Biology and Ecology, **185:** 109-129.

Srivastava, D. **S.,** 1999. Using local-regional plots to test for species saturation: Pitfalls and potentials. Journal of Animal Ecology, 68: 1-16.

Whittaker, **R.** H., 1972. Evolution and measurement of species diversity. Taxon, 21:213-51.