Parataxonomy: a test case using beetles

C. G. Majka & S. Bondrup–Nielsen

Abstract

Parataxonomy: a test case using beetles.— The present study examines the utility of parataxonomic sorting (groupings of similar individuals, categorized by non–experts, relying on features of external morphology) using data from a study of beetle communities in four forest habitats in Nova Scotia, Canada. Alpha diversity and the Shannon–Weaver, Simpson, Berger–Parker, and Brillouin indices of diversity, derived from both taxonomic species and parataxonomic units, are compared and yield identical habitat rankings. Beta diversity rankings derived from both data sets do not differ although they produce slightly different rankings. The Elateridae, Curculionidae, Cantharidae, and Staphylinidae had particularly large numbers of "lumping" and "splitting" errors. Although the overall gross sorting error was only 14%, individual families of beetles had errors between 0% and 200% with an average error of 38%. The limitations of the parataxonomic approach are discussed; both in regard to the practical application of the concept, as well its theoretical basis. We note the spillover of this discourse to the subject of what constitutes a species and observe that this discussion has been misplaced due to the unfortunate confusion of the two usages of the term "morphospecies".

Key words: Parataxonomy, Morphospecies, Beetles, Biodiversity, Conservation, Ecological management.

Resumen

Parataxonomía: argumentación sobre los test, utilizando escarabajos.— El presente estudio examina la utilidad de la ordenación parataxonómica (agrupación de individuos similares, categorizados por aficionados, basada en caracteres morfológicos externos) usando los datos de un estudio de comunidades de escarabajos de cuatro hábitats forestales de Nueva Escocia, Canadá. Se comparan la diversidad alfa y los índices de diversidad de Shannon–Weaver, Simpson, Berger–Parker y Brillouin, obtenidos tanto de especies taxonómicas como de unidades parataxonómicas, dando como resultado rankings de hábitats idénticos. Los rankings de diversidad beta procedentes de ambas series de datos no se diferencian, aunque arrojan rankings ligeramente distintos. Los Elateridae, Curculionidae, Cantharidae y Staphylinidae presentaban gran cantidad de errores de "agrupación" y "escisión". Aunque el error de clasificación bruto global era tan solo del 14%, algunas familias de escarabajos presentaban errores de entre el 0 y el 200%, con un error medio del 38%. Se discuten las limitaciones del planteamiento parataxonómico; tanto en lo que hace referencia a la aplicación práctica del concepto, como a su base teórica. Esta discusión nos lleva al tema de en qué consiste una especie y nos permite ver como esta discusión ha sido mal enfocada debido a la desafortunada confusión de los dos usos del término "morfoespecie".

Palabras clave: Parataxonomía, Morfoespecies, Escarabajos, Biodiversidad, Conservación, Gestión ecológica.

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Introduction

The utility of invertebrates in environmental monitoring has often been limited by two factors: 1) many invertebrate groups are very species rich and (often) inadequately known taxonomically; and 2) limited pools of taxonomic expertise exist and the learning curves to acquire such expertise can be protracted. Hence a procedure to streamline the collection of useful data in such a way as to produce repeatable results would be a desirable goal.

With this in mind Oliver & Beattie (1993, 1996a, 1996b) proposed the concept of "morphospecies" (groupings of similar individuals, categorized by non–experts, relying on features of external morphology) as a tool to rapidly classify invertebrates in the context of environmental monitoring and conservation evaluation. Oliver and Beattie's work was followed by Pik et al. (1999), Derraik et al. (2002), Barratt et al. (2003), and other empirical studies. Krell (2004) subsequently pointed out that the term "morphospecies" is properly preoccupied by a term widely used in evolutionary biology and introduced by Cain (1954). He proposed that parataxonomic unit (PU) be employed instead, a terminology which we follow in the remainder of this paper.

If this approach is validated it could provide a potentially useful technique since invertebrates can have significant utility in environmental monitoring (Rosenberg et al., 1986; Erhardt & Thomas, 1991; Kremen et al., 1993). Invertebrates are widespread, numerous, species–rich, and easily sampled. They exhibit greater site specificity than vertebrates, and often respond to environmental changes more rapidly than vascular plants or vertebrates (Oliver & Beattie, 1996a). Beetles (Coleoptera) are particularly well–suited for such purposes since in addition to being hyperdiverse and relatively easily sampled, they also include representatives of many free–living trophic guilds. If competitive exclusion as proposed by Hardin (1960) is correct, then measuring alpha diversity is indicative of the presence or absence of microhabitats occupied by each of the invertebrate species. Hence examining species richness, particularly of extremely diverse groups such as beetles, allows for an examination of at least some dimensions of the environment as seen through a very fine ecological mesh. Of course, indices of diversity are by their very nature radical simplifications. Much important ecological information, of significant potential interest in management or conservation contexts, is not conveyed by such simple measures and they should not serve as substitutes for detailed species —and population—based data that can ground management decisions in biological reality. They do, however, have utility in comparing similar sites and in monitoring changes at a site over time.

Parataxonomy has, nevertheless, proved to be a contentious and problematic approach. It has been subjected to a wide range of serious questions with respect to its theoretical soundness, how (or even if) such information one can be properly applied and interpreted, and to what groups it might be applicable (Goldstein 1997, 1999a, 1999b; Brower, 1995). Krell (2004) surveyed a series of studies that evaluated the parataxonomic approach and offered a comprehensive theoretical examination of the concept. He showed that parataxonomic sorting errors depend not only on the taxonomic group in question, but also on the sorter and the sample, leading him to conclude that sorting error is itself not predictable. Furthermore, philosophical and theoretical considerations indicate that parataxonomy does not fulfill the criteria of a scientific method. Such empirical and theoretical considerations lead him to exclude parataxonomy from a large spectrum of potential uses noting, however, that it is propedeutic and can be a heuristically valuable tool for determining patterns in taxonomically neglected groups. Consequently, Krell (2004) argued that PUs provide limited, but adequately accurate, data for: a) global comparisons of gross species richness; and b) non–comparative descriptions of species richness of single sites or comparisons of species numbers of different habitats within one area without considering species overlap.

The present study further investigates the parataxonomic approach in the context of the latter area, employing a set of Coleoptera data from the temperate, Nearctic region. Kehler et al. (1996, 2004) conducted a study of forest beetles caught in flight–intercept traps in four different forested habitats in Nova Scotia, Canada. The specimens were sorted into PUs (called "morphospecies" by the sorters) by non–experts roughly in accordance with the protocols of Oliver & Beattie (1993). Since that time, much of the collection has been donated to the Nova Scotia Museum and the first author (with the assistance of other experts in Coleoptera taxonomy) has completed the taxonomic determination of the specimens. Thus, it is now possible to assess the accuracy of the original PU data set.

Material and methods

Coleoptera sampling took place in central Nova Scotia within an area 300 km long by up to 100 km wide (Kehler et al., 1996, 2004). Sampling was conducted in both 1994 and 1995, although only the 1995 data are considered in this paper. In 1995, 10 softwood and 10 hardwood stands were sampled. Four forest categories were distinguished; old softwood (OSW), young softwood (YSW), old hardwood (OHW), and young hardwood (YHW). Softwood stands were defined as having more than 70% coniferous trees [principally red spruce (*Picea rubens* Sarg.) and balsam fir (*Abies balsamea* L.) Mill (Pinaceae)]. Hardwood stands were defined as having more than 70% deciduous trees [principally sugar maple (*Acer saccharum* Marsh.), red maple (*Acer rubrum* L.) (Aceraceae), yellow birch (*Betula alleghaniensis* Britt.) and white birch (*Betula papyrifera* Marshall) (Betulaceae)]. All stands were greater than 2.5 hectares, and were at least 300 m

from any road. Sampling for beetles was carried out at distances at least 50 m from the stand boundary. Window flight–intercept traps were used to sample for beetles.

Sorting and classification was carried out on the basis of external morphology by individuals without particular knowledge or expertise in Coleoptera (as per the protocols of Oliver & Beattie, 1996a). While some effort was made at the time to attach Latin binomials to some of these "morphospecies" (Kehler et al., 1996) subsequent analysis (Kehler et al., 2004) treated them as PUs (apparently due to oversight, Kehler et al., 1996, 2004) neglected to include specimens of *Byturus unicolor* Say (Byturidae) in their analysis. Since this species was abundant in many of the OHW and YHW stands, their inclusion in the calculations of diversity indices affects diversities in these two stand types. Unfortunately some of these specimens were not preserved hence it was not possible after the fact to exactly determine the exact number collected. Consequently this species was excluded from the calculations to allow for comparisons of taxonomic species to PUs). Subsequently the first author examined the extant material (some specimens had either been discarded, dispersed, or were unavailable for examination) and determined them to taxonomic species.

From these data the alpha diversities for each of the 20 forest stands were derived, as were average stand diversities for the four forest types. To further examine dimensions of biotic diversity at the stand level, several indices of diversity were calculated for each stand as well as cumulatively for each forest category:

1. The Shannon–Weaver Diversity Index (Shannon & Weaver, 1949) is an information index that reflects both the equitability and evenness of a sample. It is affected by the randomness of sampling and is defined as:

$$H' = - \sum_{i=1}^{s} p_i \log p_i$$

where p_i is the proportion of the community that belongs to the ith species.

2. The Simpson Index of Diversity (Simpson, 1949), a dominance index, emphasizes the abundance of the more dominant species in a sample. It is defined as:

$$\lambda = \sum p_i^2$$

where p_i is the proportion of the community that belongs to the ith species.

3. The Brillouin Index of Diversity (Brillouin, 1962) is a more effective measure of diversity in circumstances where the randomness of a sample cannot be guaranteed. It is defined as:

$$H_B = \frac{\ln N! - \sum \ln n_i!}{N}$$

where N is the total number of individuals and n_i is the number of individuals in the ith species.

4. The Berger–Parker Index represents a different approach that is strongly influenced by the evenness of the sample. It is readily calculated as the largest species proportion of all species in a community thus:

$$d = p_{MAX} \ (\forall i: p_{MAX} \geq p_i)$$

where p_i is the proportion of the community which belongs to the ith species, and p_{MAX} is the largest such proportion.

The forest stands were ranked in terms of increasing taxonomic alpha diversity. This was compared to the ranking order derived from the PU data. The ratio of the diversity indices among the forest stands were compared between taxonomic species and PUs using a G–test.

5. Beta Diversity: because there were large differences between the faunal compositions of the different forest stand types (on average each stand type shared only 45% of its fauna with any other stand type) it was decided to employ Coefficient of Community (CC) (Whittaker, 1972) to measure beta diversity, recommended by Pielou (1974) as being applicable in such situations. Coefficient of Community (CC) was calculated as:

$$CC = \frac{200s_{xy}}{s_x + s_y}$$

where s_x is the number of species in habitat X; s_y is the number of species in habitat Y; and s_{xy} is the number of species in common to both habitats X and Y. Beta Diversity was compared using a non–parametric Mann–Whitney U test.

The correspondence ratio (accuracy) of taxonomic species to PUs, as per Oliver & Beattie (1996a) was calculated. Frequencies of lumping, splitting, and one–to–one correspondence derived in this study were compared to frequencies reported in Oliver & Beattie (1996a) and Derraik et al. (2002). The gross sorting error (as per Krell, 2004) for each family of Coleoptera was also calculated.

Results

Table 1 shows alpha, Shannon–Weaver, Simpson, Berger Parker, and Brillouin index of diversity values for all four forest composition categories. For both taxonomic species and PUs, the ranking of all categories remained invariant as (in increasing richness) YSW → OSW → OHW → YHW when calculated by all diversity measures. The only exception was the Brillouin values for OSW and OHW which, although very similar, were in reverse order. These results are noteworthy because the ratio of correspondence (accuracy) of sorting in this study is decidedly lower than in Oliver & Beattie (1996a). Figure 1 shows the frequency values of these from this study as well as, for comparison, the values from Oliver & Beattie (1996a) and Derraik et al. (2002). Categories on

Table 1. Alpha diversity and diversity indexes: Tx. Taxonomic; PU. Parataxonomic units; SE. Standard error; YSW. Young Softwood; OHW. Old Hardwood; OSW. Old Softwood; YHW. Young Hardwood; [1] Adjusted G–test.

Tabla 1. Diversidad alfa e índices de diversidad: Tx. Taxonómico; PU. Unidades parataxonómicas; SE. Error estándar; YSW. Madera blanda joven; OHW. Madera dura vieja; OSW. Madera blanda vieja; YHW. Madera dura joven; [1] Test G ajustado.

	Shannon–Weaver		Simpson $(1/\lambda)$		Berger–Parker $(1/d)$		Brillouin Index		Alpha (mean±SE)	
	Tx	PU	Tx	PU	Tx	PU	Tx	PU	Tx	PU
YSW	3,635	3,406	15,088	10,461	4,430	3,488	4,754	4,405	29,2±1.14	23,2±1.63
OHW	3,886	3,693	21,622	18,836	6,151	5,780	5,263	4,999	48,8±3.86	38,4±2.47
OSW	3,996	3,804	27,336	22,339	6,921	5,849	5,277	4,949	37,2±3.18	28,4±2.18
YHW	4,066	3,810	32,915	22,922	9,865	9,414	5,498	5,082	52,2±2.61	52,2±2.61
G–test[1]	0,000		0,395		0,066		0,001			
Prob.	>> 0.05		>> 0.05		>> 0.05		>> 0.05			

the x–axis to the left of "1–to–1" represent "lumping"; those to the right represent "splitting". In Oliver & Beattie (1996a), the one–to–one correspondence of taxonomic species to PUs was 80% while in Derraik et al. (2002) it was 62.8%. In this study the accuracy is 67% with roughly equal distribution tails of lumping (16.7%) and splitting (15.9%).

Four families, Elateridae, Curculionidae, Cantharidae, and Staphylinidae, accounted for 60% of the errors, and of these, the former two combined accounted for 42% (table 2). All four are species–rich families with many superficially similar members, differentiated by characters that may not be obvious to the non–expert. The number of taxonomic species and PUs for each family of Coleoptera is shown in table 3 as is the gross error of PU sorting (as per Krell, 2004). Although the overall gross error is only 15%, values for individual families range between 0% and 200% with a mean value of 38%.

Beta diversity as calculated by the Coefficient of Community (CC) method is shown in table 4. In this study the parataxonomic approach narrowly fails in producing the same ranking derived from taxonomic species. Beta diversity appeared higher using the taxonomic approach (mean (± S.E.) of 50.7 ± 3.70) versus the parataxonomic approach (mean (± S.E.) of 43.2 ± 2.42) but did not differ statistically (U = 10.0, p = 0.20). The ratio of the Beta diversities (see table 4) was not significantly different (adjusted G–test = 0.637, p << 0.05). The correlation between the two approaches based on the Beta diversity values presented in table 3 is 0.93 with a significance of 0.01. Nonetheless the results may indicate that at the 67% level of one–to–one taxonomic–to–parataxonomic correspondence (fig. 1) of the present study, beta diversity may begin to loose utility.

Discussion

The results of this study indicate that the parataxonomic approach is surprisingly robust. Even at a 67% level of accuracy, the rankings of the four different types of forest stands —Young Softwood (YSW), Old Hardwood (OHW), Old Softwood (OSW), and Young Hardwood (YHW)— are preserved between taxonomic and parataxonomic approaches. This agrees with Oliver & Beattie (1996a) in which the ranking of the four habitats (dry, grassy, moist, and rain–forests), measured in terms of alpha and beta diversity, were preserved for taxonomic and parataxonomic data.

Beta diversity, as measured by the Coefficient of Community approach, appears, however, to have begun to deviate from a ranking correspondence although the ranks do not differ statistically. In the current study the accuracy is 67%. It may be that below this level of accuracy beta diversity ranking will not be conserved.

Although in this study the Elateridae and Cantharidae join the Staphylinidae, Curculionidae, and Scydmaenidae identified by Oliver & Beattie (1996a) as problematic groups for this approach, Krell's (2004) survey of various studies employing parataxonomic sortings makes it clear that there is significant variability in accuracy from study to study, depending on sample and sorter. Many other groups surveyed by Krell (2004) show large and variable values in terms of gross sorting error. Consequently sorting error is not a predictable value for a taxonomic group, making it difficult if not impossible to generalize for which groups the parataxonomic approach is amenable. Krell (2004) further reports the sorting accuracy for 11 studies (the only ones which he could find in the literature)
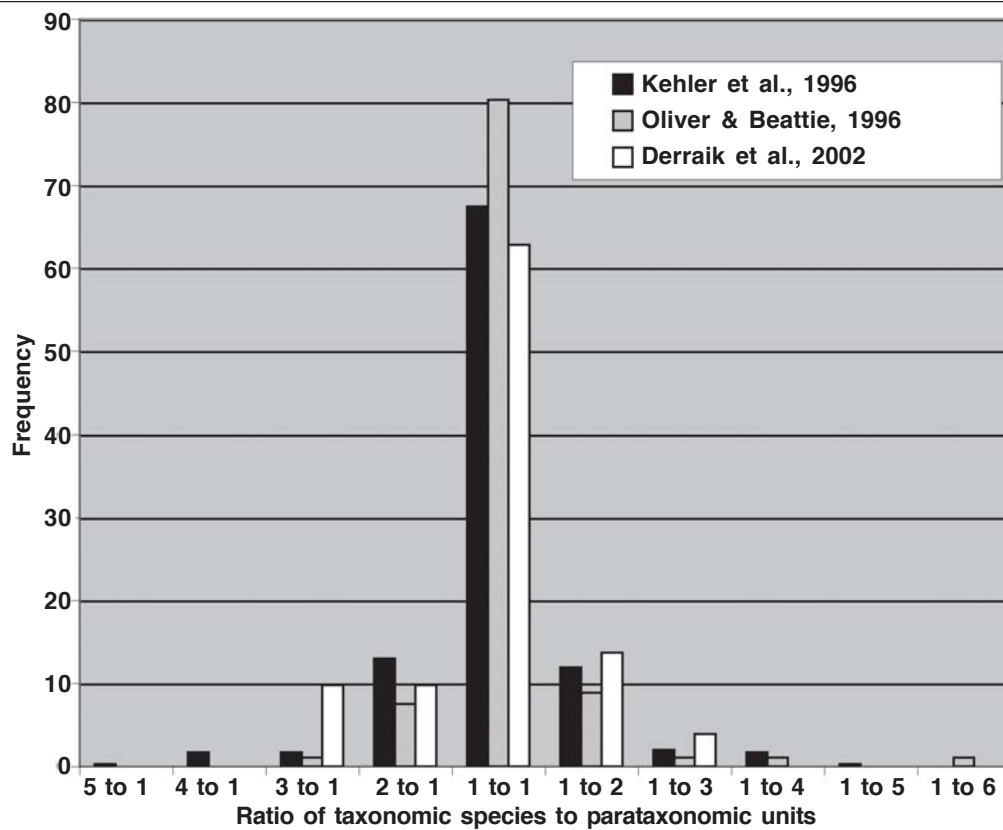
Fig. 1. Taxonomic species to parataxonomic unit correspondence.

Fig. 1. Correspondencia entre especies taxonómicas y unidades parataxonómicas.

Table 2. Lumping and splitting errors by family: Sp. % of species; L. Lumped; S. Split. T. Total.

Tabla 2. Errores de agrupamiento y escisión por familias: Sp. % de especies; L. Agrupadas; S. Escindidas. T. Total.

Family	Sp	L	S	T
Elateridae	41	10	10	20
Curculionidae	29	8	10	18
Cantharidae	10	5	4	9
Staphylinidae	21	4	3	7
Cerambycidae	17	3	2	5
Carabidae	9	1	3	4
Nitidulidae	8	3	1	4
Coccinellidae	5	1	2	3
Mordellidae	8	0	3	3
Erotylidae	2	1	1	2

Family	Sp	L	S	T
Leiodidae	6	1	1	2
Melandryidae	8	1	1	2
Scarabaeidae	10	1	1	2
Anobiidae	5	1	0	1
Kateretidae	1	0	1	1
Chrysomelidae	8	0	1	1
Dermestidae	1	1	0	1
Lycidae	3	0	1	1
Salpingidae	1	1	0	1
Total	193	42	45	87

Table 3. Number of taxonomic species (Tx) and paratxonomic units (PU) for each family of Coleoptera: GE. Gross error (l(A–B)/Al(%)).

Tabla 3. Número de especies taxonómicas (Tx) y unidades parataxonómicas (PU) de cada familia de Coleoptera: GE. Error bruto (|(A–B)/A|(%)).

Family	Tx	PU	GE	Family	Tx	PU	GE
Anobiidae	5	3	40	Lycidae	3	3	0
Apionidae	1	0	100	Melandryidae	8	6	25
Byturidae	1	1	0	Monotomidae	1	1	0
Cantharidae	10	10	0	Mordellidae	8	3	63
Carabidae	9	4	56	Mycetophagidae	1	0	100
Cerambycidae	17	16	6	Nitidulidae	8	12	50
Cerylonidae	1	1	0	Oedemeridae	1	1	0
Chrysomelidae	9	8	11	Orsodacnidae	1	0	100
Ciidae	5	0	100	Pyrochroidae	1	1	0
Cleridae	1	1	0	Pythidae	1	1	0
Coccinellidae	5	6	20	Salpingidae	1	0	100
Cryptophagidae	1	0	100	Scarabaeidae	10	7	30
Curculionidae	29	36	24	Scirtidae	4	3	25
Dermestidae	1	3	200	Scraptidae	5	0	100
Dytiscidae	1	1	0	Silphidae	5	3	40
Elateridae	41	33	20	Silvanidae	2	1	50
Endomychidae	3	1	67	Sphindidae	1	0	100
Erotylidae	2	2	0	Staphylinidae	21	23	10
Eucinetidae	1	0	100	Stenotrachelidae	1	1	0
Eucnemidae	2	1	50	Tenebrionidae	4	5	25
Hydrophilidae	1	1	0	Tetratomidae	4	3	25
Kateretidae	1	1	0	Trogidae	1	1	0
Lampyridae	5	2	60	Trogossitidae	1	1	0
Leiodidae	6	7	17	Total	253	216	15
Lucanidae	2	2	0	Mean of families			38

with values ranging between 23% and 92%. Krell (2004) points out that this value this is of considerable importance in evaluating the parataxonomic approach. In one instance, Oliver & Beattie (1993) reported a Bryophyta sorting with only a 1% error; however, the accuracy of the sorting was only 23%, indicating a serendipitously equal number of splittings and lumpings. Such situations led Krell (2004, pp. 797) to conclude that, "It may be seriously questioned if a high level of inaccuracy in a sorting result is acceptable if the gross error is low, because the low overall error is caused only by good luck". Although in the present study the overall gross error of the sorting is only 15%, values for individual families range between 0% and 200% with a mean

error of 38% (table 3). This is almost double the mean sorting error of 22% in the 79 sortings surveyed by Krell (2004).

There are also unresolved questions as to what significance diversity measurements in general can have in relation to conservation objectives. Goldstein (1997, 1999a) argues that any ecosystem approach that decouples species– and population–specific requirements from management strategies risks compromising fundamental conservation objectives. Wheeler (1995, pp. 481) argues for the inclusion of systematics within diversity calculations in saying, "more informative measures of biodiversity take into account both numbers of species and the cladistic diversity that they represent".

Table 4. Beta diversity values: Tx. Taxonomic species; PU. Parataxonomic units. (For other abbreviations see table 1.)

Tabla 4. Valores de la diversidad beta: Tx. Especies taxonómicas; PU. Unidades parataxonómicas. (Para las otras abreviaturas ver la tabla 1.)

	OHW & YSW	YHW & YSW	OSW & YSW	OHW & OSW	OSW & YHW	OHW & YHW
Tx	39,29	41,59	50,49	52,50	57,02	63,08
PU	38,34	35,82	45,20	42,16	45,28	52,63

We are cogniscent of such concerns, and they apply in large measure to indices of diversity however calculated. Clearly any index of diversity is but one approach that attempts to illustrate a small subset of an ecosystem's properties. It should not be used as a substitute for more detailed and species–based information, particularly in a management or conservation context. The concerns raised by Goldstein (1997, 1999a) make clear the potential pitfalls of conservation approaches based solely on the management of emergent properties of ecosystems or of ecosystem processes. Differences in diversity indices between sites, or changes in diversity over time, should serve as a springboard for further investigation —not as a substitute for it.

Another broad area of concern is with respect to the fundamental epistemological nature of parataxonomy as a discipline. Popper (1989) proposed two principal criteria which a research activity must meet in order to be considered a science: 1) falsifiability; and 2) inter–subjective testability due to reproducibility. Krell (2004) evaluated parataxonomy on these grounds and found that it does not meet the criteria of being a scientific method. This constitutes a serious limitation to the utility of the parataxonomic approach. Bearing this in mind Krell (2004) carefully delineated the spheres where the parataxonomic approach is of utility as being: a) global comparisons of gross species richness; and b) non–comparative descriptions of species richness of single sites or comparisons of species numbers of different habitats within one area without considering species overlap.

Oliver & Beattie (1996a) proposed morphospecies as a relatively quicker and less expensive surrogate for taxonomic species in environmental monitoring and conservation contexts. Nonetheless, even in contexts where the parataxonomic approach is of utility, the savings realized on the one hand may mean that results are only of a more limited applicability on the other —something that ecologists and environmental managers should bear in mind in designing studies.

Some of the debate around this issue has spilled over into the discussion of what constitutes a species and what sort of information we are seeking from nature when we apply any sort of taxonomic system to it. This is a complex question with an extensive philosophical and biological literature. Mayden (1997) enumerated and discussed 22 different concepts of "species" in use today. This discussion has perhaps been fueled by a pluralist interpretation of "species" which argues that multiple non–exclusive notions are useful and can yield different kinds of information (Mayden, 1997; Ereshefsky, 1998). A corollary as argued by Stanford (1995) is that the concept of species exists only relative to a given conceptual framework. Thus species taxa have no unique and objective existence in the real world.

In large measure, however, this discussion is misplaced in this context by the unfortunate confusion between the term "morphospecies" *sensu* Cain (1954) and "morphospecies" *sensu* Olivier & Beattie (1993, 1996a, 1996b). As Krell (2004) has pointed out this latter usage is erroneous, not only because the latter is properly preempted by the former, but also what is being considered is not a "pecies" in any meaningful sense of the term, but rather the result of a parataxonomic sorting.

While this philosophical backdrop may not have a direct bearing on evaluating the empirical utility of parataxonomy, it does bear on the more general understanding of the kind of information we derive from nature in employing any analytic grid of classification. How useful it is, is something that we can assess. How real it is, is subject to interpretation.

R e f e r e n c e s

Barratt, B. I. P., Derraik, J. G. B., Rufaut, C. G., Goodman, A. J. & Dickinson, K. J. M., 2003. Morphospecies as a substitute for Coleoptera species identification, and the value of experience in improving accuracy. *Journal of the Royal Society of New Zealand*, 33: 583–590.

Brillouin, L., 1962. *Science and Information Theory, 2nd edition.* Academic Press, New York, USA.

Brower, A. V. Z., 1995. A reply to Oliver and Beattie. *Trends in Ecology and Evolution*, 10: 204.

Cain, A. J., 1954. *Animal Species and their Evolution.* Hutchinson's Univ. Library, London, England.

Derraik, J. G. B., Closs, G. P., Dickinson, K. J. M, Sirvid, P., Barratt, B. I. P. & Patrick, B. H., 2002. Arthropod morphospecies versus taxonomic species: a case study with Aranae, Coleoptera, and Lepidoptera. *Conservation Biology*, 16: 1015–1023.

Erhardt, A. & Thomas, J. A., 1991. Lepidoptera as indicators of change in the semi–natural grasslands of lowland and upland Europe. In: *The conservation of insects and their habitats*: 213–237 (N. M. Collins & J. A. Thomas, Eds.). Academic Press, London.

Goldstein, P. Z., 1997. How many things are there? A reply to Oliver and Beattie, Beattie and Oliver, Oliver and Beattie, and Oliver and Beattie. *Conservation Biology*, 11: 571–574.

– 1999a. Functional ecosystems and biodiversity buzzwords. *Conservation Biology*, 13: 247–255.

– 1999b. Clarifying the role of species in ecosystem management: a reply. *Conservation Biology*, 13: 1515–1517.

Hardin, G., 1960. The competitive exclusion principle. *Science*, 131: 1292–1297.

Kehler, D., Corkum, C. & Bondrup–Nielsen, S., 1996. *Habitat associations and species diversity of forest beetle communities of Nova Scotia. Centre for Wildlife and Conservation Biology.* Acadia Univ., Canada.

– 2004. Beetle diversity associated with forest structure including deadwood in softwood and hardwood stands in Nova Scotia. *Proceedings of the Nova Scotian Institute of Science*, 42(2): 227–239.

Kremen, C., Colwell, R. K., Erwin, T. L., Murphy, D. D., Noss, R. F. & Sanjayan, M. A., 1993. Terrestrial arthropod assemblages: their use in conservation planning. *Conservation Biology*, 7: 796–808.

Krell, F.–T., 2004. Parataxonomy vs. taxonomy in biodiversity studies – pitfalls and applicability of "morphospecies" sorting. *Biodiversity and Conservation,* 13: 795–812.

Mayden, R. L., 1997. A hierarchy of species concepts: the denouement in the saga of the species problem. In: *Species: the units of biodiversity*: 381–424. (M. F. Claridge, H. A. Dawah & M. R. Wilson, Eds.). Chapman & Hall, Melbourne.

Oliver, I. & Beattie, J. A., 1993. A possible method for the rapid assessment of biodiversity. *Conservation Biology*, 7: 562–568.

– 1996a. Invertebrate morphospecies as surrogates for species: a case study. *Conservation Biology*, 10: 99–109.

– 1996b. Designing a cost–effective invertebrate survey: a test of methods for rapid assessment of biodiversity. *Ecological Applications*, 6: 594–607.

Pielou, E. C., 1974. *Population and community ecology*. Gordon and Breach Science Publishers, New York.

Pik, A. J., Oliver, I. & Beattie, A. J., 1999. Taxonomic sufficiency in ecological studies of terrestrial invertebrates. *Australian Journal of Ecology*, 24: 555–562.

Popper, R. 1989. *Logik der Forschung*, 9th edition. Mohr, Tübingen, Germany.

Rosenberg, D. M. H., Danks, H. V. & Lehmkuhl, M., 1986. Importance of insects in environmental impact assessment. *Environmental Management*, 10: 773–783.

Shannon, C. E. & Weaver, W., 1949. *The mathematical theory of communication*. Urbana IL: University of Illinois Press.

Simpson, E. H., 1949. Measurement of diversity. *Nature,* 163: 688.

Stanford, P., 1995. For pluralism and against realism about species. *Philosophy of Science*, 62: 70–91.

Wheeler, Q. D., 1995. Systematics, the scientific basis for inventories of biodiversity. *Biodiversity and Conservation*, 4: 476–489.

Whittaker, R. H., 1972. Evolution and measurement of species diversity. *Taxon*, 21: 213–251.