Biodiversity and Conservation (2005) 00:00–00
DOI 10.1007/s10531-005-2931-5

Efficiency of a rapid assessment of the diversity of ground beetles and ants, in natural and disturbed habitats of the Nahuel Huapi region (NW Patagonia, Argentina)

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Received 17 August 2004; accepted in revised form 15 February 2005

Key words: Ants, Beetles, Extrapolation, Patagonia, Rarefaction, Species richness

Abstract. We use sample-based rarefaction curves to evaluate the efficiency of a rapid species richness assay of ground beetles and ants captured in pitfall traps in the Nahuel Huapi National Park (NW Patagonia, Argentina). We ask whether ant species richness patterns show some concordance with those of beetles, and use several extrapolation indices for estimating the expected number of species at a regional scale. A total of 342 pitfall traps were spread in groups, at an intensity of 9 traps/100 m^2, with two collection stations, at each of 19 sites representative of burned and unburned habitats in the forest, scrub and steppe, along a west-to-east transect of 63 km long. The high regional habitat heterogeneity along the west-to-east gradient is paralleled by a turnover of beetle and ant species, although different families of Coleoptera show idiosyncratic responses across habitat types. Spatial stratification of sampling over three major habitats along with the inclusion of burned and unburned environments may improve sampling efficiency. The observed and extrapolated species richness suggests that we captured a high proportion of the total number of species of beetles and ants known for the region. However, trends in species richness of ants may not indicate similar trends in beetles. Ants and beetles cannot be used as surrogate taxa for the analysis of species richness patterns. Instead, both taxa should be considered as focal as they may offer complementary information for the analysis of the effect of disturbance and regional habitat heterogeneity on species diversity patterns at a regional scale.

Completing a full inventory of the earth's biota is an urgent priority (e.g., Ronquist and Gärdenfors 2003). The main challenge is documenting species richness patterns of the hyper-diverse and poorly known groups (e.g., Hammond 1992, 1994) and exploring wild regions of the world where intact habitats of high conservative value remain poorly known (Mittermeier et al. 2003). However, several of such regions (e.g., Amazonia, Chaco, Patagonia, Magellanic forests: see Mittermeier et al. 2003 for details) are in South American countries that usually lack sufficient economic resources and researchers devoted to the analysis of biodiversity. Under these circumstances, it is essential to implement adequate protocols to objectively evaluate the efficiency and completeness of rapid diversity assessments. One of the basic problems is how to estimate the actual number of species in heterogeneous regions given that it is not possible to count every individual, or to sample everywhere (see e.g., Rosenzweig et al. 2003 for discussion). Another problem is that as more individuals are sampled, more species are recorded; hence, there is an effect of abundance and sample effort on species richness measures and comparisons (Gotelli and Colwell 2001).

Fortunately at present, there are a number of techniques to address such issues, collectively referred to as taxon sampling curves (*sensu* Gotelli and Colwell 2001). More specifically, accumulation and rarefaction curves represent useful tools to evaluate the completeness and efficiency of species richness assessments. They provide reliable measures of species richness based on standardized measures of sampling effort that allow valid comparisons among different habitats and/or different kinds of sampling methods for critical evaluation of ecological theory (for reviews and examples see Colwell and Coddington 1994; Longino and Colwell 1997; Gotelli and Colwell 2001; Rosenzweig et al. 2003). On the other hand, given that the number of species observed in field samples will always be lower than the actual number of species, several indices have been developed to estimate an expected value of species richness for any given region by extrapolation from a limit number of samples taken from the same region (see Colwell and Coddington 1994; Hammond 1994; Gotelli and Colwell 2001; Rosenzweig et al. 2003).

In the present paper, we use sample-based rarefaction curves re-scaled to individuals (Gotelli and Colwell 2001) to evaluate the efficiency and completeness of a rapid and low-cost species richness assay of ground beetles and ants captured in pitfall traps in the Nahuel Huapi National Park (NW Patagonia, Argentina). Ants represent a less-diverse and relatively well-known group in NW Patagonia, as compared to the relatively poorly known and highly diverse beetles. The number of ant species known from western Patagonia is about 23 species (e.g., Kusnesov 1953, 1959). This is one order of magnitude less than the diversity expected for beetles within the same region, although the actual number of beetle species inhabiting the region is unknown (Roig-Juñent, personal communication). Ant species are also usually easy to identify by non-specialists, and this makes them suitable to consider as a likely candidate for a focal group (Hammond 1994). The question is, however, whether ant species richness patterns, as expressed by taxon sampling curves, show some concordance with those of beetles within the same studied region. The strategy of identifying taxa whose diversities are correlated with the diversity of other groups or show similar responses to environmental gradients or disturbances has been useful in other regions of the world (e.g., Australia: Oliver and Beattie 1996a) as a way to optimize the search for a representative ‘shopping basket’ of taxa that together serve as a composite focal group (see

Hammond 1994). In the present analysis, we offer evidence to evaluate whether ants and beetles may be considered surrogate taxa for each other in analysis of species diversity patterns within the studied region.

Throughout the present analysis, we emphasize the need for any insect species richness assay in NW Patagonia to take into account the high environmental heterogeneity, determined by presence of different ecological units (see ‘Area of Study’ section), as well as the effect of fire, of both natural and anthropogenic origin, which has played a major role in the vegetation structure of the local landscapes (see Kitzberger 2003; Veblen et al. 2003 for review). The interplay between those two factors might have occurred at different geographic and temporal scales to account for the spatial variation in insect species diversity within the region (see e.g., Farji-Brener et al. 2002). However, given a situation where budget restrictions limit the possibility of sampling to only one season and to a relatively small number of collection stations, we ask what kind of sampling strategy (i.e., sampling in only one habitat vs. over different habitats; in natural habitats vs. in disturbed habitats) could be more efficient to capture the greater diversity of ants and beetles relative to sampling effort. To answer this question, we compare combined-habitat rarefaction curves to within-habitat rarefaction curves. If, after re-scaling to the accumulated number of individuals, the combined-habitat curves were steeper than the within-habitat curves, this would indicate turnover of species among habitats. This would suggest spatial stratification of sampling as suitable strategy to improve the efficiency of insect species richness assays within the studied region (see also Longino and Colwell 1997). In the same way, we compare disturbed-habitat rarefaction curves to undisturbed-habitat rarefaction curves to evaluate the added value of considering both types of environments in the design of a sampling strategy for an insect species richness assay within the studied region.

We examine the performance of several extrapolation indices to estimate the expected number of beetle and ant species within the region studied. At present, there is no consensus about what indices perform best for different situations (i.e. different taxa or places). The strategy of modeling sampling protocols for different datasets to evaluate objectively the performance of extrapolation indices is still in its infancy (see Rosenzweig et al. 2003 for an exception). For real situations, where the sampling universe is unknown (as in the case of the present analysis), there is at least the possibility of evaluating empirically the performance of different estimators. For instance, if the species richness estimator stabilizes, tends to converge with the observed species richness and is independent of sample size or the number of individuals, it is more likely to be a reliable estimate of total species richness for any given region (e.g., Palmer 1990; Gotelli and Colwell 2001). Complementary analyses include evaluating the completeness of our survey by examining patterns in rare species accumulation curves. Longino and Colwell (1997) suggest that inventories of hyper-diverse groups may never be complete in the strict sense; they can only reach some arbitrarily defined low rate of new species accrual per unit effort. In the present analysis, we use smoothed sample-based rare species accumulation curves, rescaled to individuals, to evaluate the extent to which the number of rare species revealed by our passive sampling method tends to stabilize with increasing sampling effort.

Overall, the present analysis provides useful information around the issue of how to improve the efficiency of insect species richness assays, i.e. how to capture the greater insect species diversity relative to sampling effort, within the studied region. Note, however, that we are not focused on community characterization neither we attempt to analyze the effect of fire on structuring community organization (cf. Farji-Brener et al. 2002). In the present analysis, we are focused exclusively on the sampling-issue. In this regard, we provide useful information for the design of cost-effective strategies to capture the greater number of species in rapid, low-cost insect diversity assessments. As a whole, we hope that the present analysis can contribute towards the elaboration of generalized sampling protocols of insect species diversity in temperate habitats of Patagonia.

Methods

Area of study

The present study was conducted in 2001 along a west-to-east transect of 63 km long within the Nahuel Huapi National Park, near Bariloche, in Argentina (40°20′–41°35′ S and 71°–72° W). The region is on the eastern flank of the Andes, close to the international border between Argentina and Chile, and within the cool–warm temperate zone. The mean annual temperature is 8 °C, though temperature can fluctuate from a mean minimum of −2 °C in the coldest month (July) to a mean maximum of 23 °C in the warmest one (January). The Andean mountains act as a barrier to the westerly airflow at temperate latitudes, resulting in a pronounced eastward rainshadow. The humid winds from the Pacific rise up and across the Andean crests causing the most intense rainfalls on the western (Chilean) side of the Cordillera and a marked W-E gradient on the eastern (Argentinean) side. Actually, in Argentina, the mean annual precipitation declines from >3000 mm in the western zone of the Nahuel Huapi National Park to <500 mm in the eastern zone, located approximately 100 km apart from the international limit toward the east (Barros et al. 1983).

Major climatic, soil and biotic differences along the west-to-east gradient allow the distinction of three major ecological units, namely: forest, scrub and steppe. In the western zone of the Nahuel Huapi National Park, there are temperate rainforests, dominated by *Nothofagus* species, which grow in sites of 3500–1500 mm of mean annual precipitation. Semi-arid scrub vegetation and forests of *Austrocedrus chilensis* (D. Don) Pic. Serm. and Bizzarri and *Nothofagus antarctica* (G. Forst.) Oerst mixed with abundant shrubs, grow along the foothill zone, in sites of 1800–1400 mm of mean annual precipitation. In the eastern zone, the steppe lacks tall vegetation except for small groups or single isolated trees. It is mainly composed of xerophytic shrubs and herbs that grow in sites of 800–600 mm of mean annual precipitation. Other references should be consulted for a more detailed description of the local vegetation and flora (Cabrera 1939; Dimitri 1974; Mermoz et al. 2000), fauna (Chehébar and Ramilo 1989; Mermoz et al. 2000), climate (Barros et al. 1983) and Quaternary biogeography (Clapperton 1993).

Choice of sampling sites and sampling method

Nineteen sites were selected along the west-to-east transect of 63 km long to capture the spatial turnover of major ecological units within the region. The selection was based on the criterion that the three major habitats were adequately represented (forest: $N = 8$; scrub: $N = 6$; steppe: $N = 5$). The potential effect of unequal sample sizes among habitats on taxon-sampling curves is corrected after randomizing the order of samples over each run during the elaboration of such curves (see Turner et al. 2000 for discussion). Given that throughout the present analysis we rescale all sample-based rarefaction and accumulation curves to the number of accumulated individuals, this makes all species richness estimations strictly comparable relative to sample effort (see Gotelli and Colwell 2001).

Sites were selected as to include replicates of disturbed (= burned) and undisturbed zones within each major ecological unit. This explains the irregular clumping of sites in Figure 1. At each site, two collection stations were established, one in disturbed and the other in undisturbed zone that in general contrast with respect to ground vegetation cover. This results in a total of 38 (19×2) collection stations for subsequent analyses. The minimum distance separating the two closest sites (Sc2 and Sc3 in Figure 1) was 300 m whereas collection stations within each site were 40 m apart from each other; these separation distances are within the range of those reported in previous studies (e.g., Porter and Savignano 1990; Rykken et al. 1997; Koivula et al. 1999; Eubanks 2001; Cook 2003), and can be assumed to provide independent information for ecological analyses (e.g., Moretti et al. 2004). Nonetheless, shuffling individuals among samples in two of the analyses performed below (i.e. F5 and $\text{MMMean}_{(\text{shuffled})}$ species richness estimations; see detailed explanation below) additionally contributes to overcoming potential effects that may come out from the spatial distribution of samples.

Beetles and ants were collected with pitfall traps, which provide a standard and replicable sampling method to study the epigaeic insect fauna, and which have been satisfactorily used in comparative studies concerned with both qualitative and quantitative data (Luff 1975; Spence and Niemelä 1994; Ausden 1999; Scudder 2000; Ribera et al. 2001). In the present analysis, a total of 342 pitfall traps were spread over the 38 collection stations, at an intensity of 9 pits$\times$100 m^2 in each collection station. Traps were plastic cups (9 cm diameter,

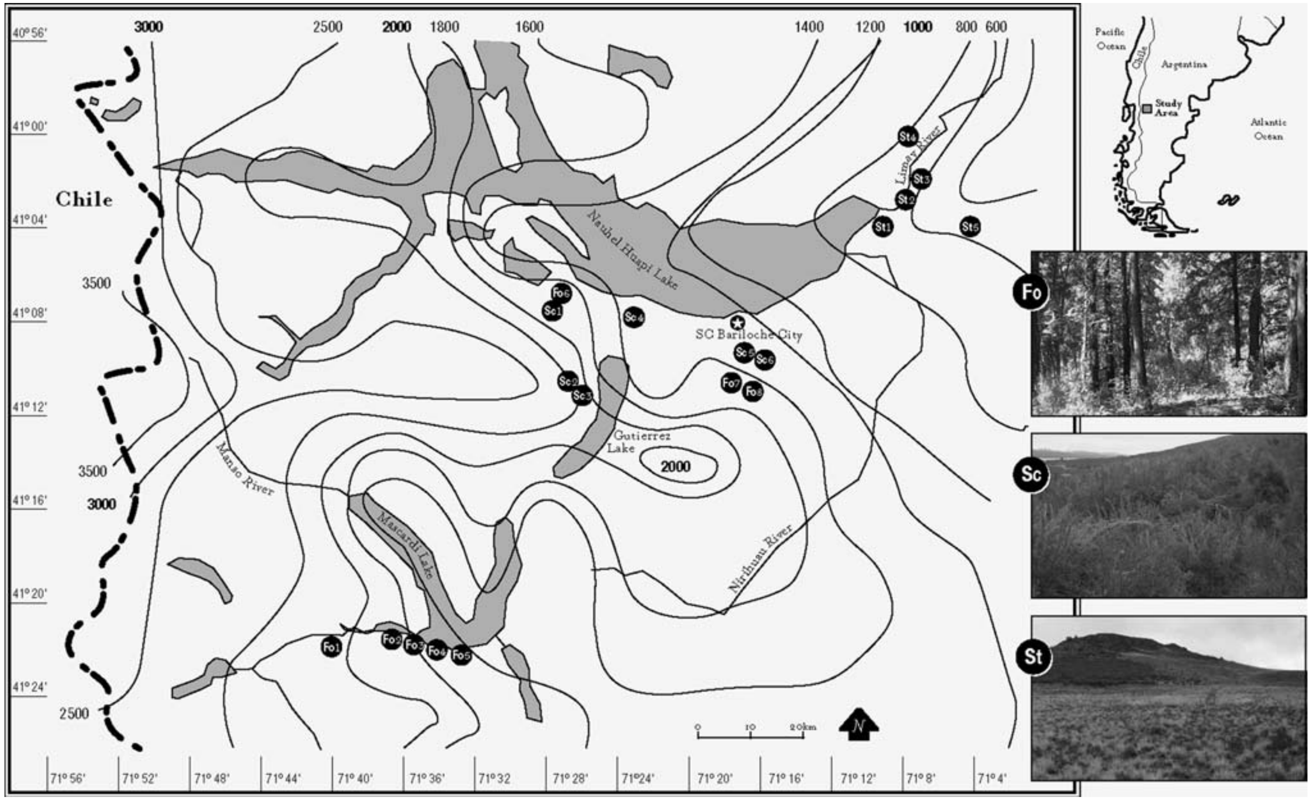

Figure 1. Area of study. The location of 19 study sites along the west-to-east transect is indicated. Isolines of mean annual precipitation are also shown. Abbreviations correspond to sites in Fo = forest, Sc = scrub and St = steppe.

12 cm depth) partly filled with water, ethylene glycol and detergent. They were opened during 3 weeks from mid January to mid February 2001 (summer) and emptied only once. The contents from the nine pits at each collection station were pooled to one sample. All samples ($N = 38$) were preserved in 70% ethyl alcohol and taken to the lab for identification of taxa.

Identification of taxa

Preliminary observation of samples with a binocular microscope (Leica MZ 7.5) allowed the separation of specimens of beetles and ants among the rest of the collected material. We used 5–25× magnification to avoid missing specimens of small-bodied taxa (e.g., Cryptophagidae). Specimens were identified to family level and, within each family, sorted to temporary morphospecies using up to 125× magnification. The use of morphospecies or recognizable taxonomic units (RTUs) as the basis for the analysis of diversity patterns in hyper-diverse or poorly known invertebrate taxa has been critically evaluated in previous studies. In general, the evidence suggests that careful use of morphospecies allow reliable assessments of insect species diversity (Oliver and Beattie 1993, 1996a, b; Beattie and Oliver 1994; Pik et al. 1999; see also Friend and Williams 1996; Lawton et al. 1998; Anderson and Ashe 2000; Bolger et al. 2000; Werner and Raffa 2000). In the present analysis, the identification of temporary RTUs was based on the analysis of morphological characters. We used identification keys published by Kusnezov (1953), Peña Guzmán (1987) and Borror et al. (1992). All the material was sent out to different professional taxonomists (see acknowledgements), who sorted out temporary morphospecies to species or confirmed their identity as morphospecies. After taxonomic determination, specimens were stored in a reference collection in the Ecotono Laboratory, National University of Comahue.

Data analysis

Evaluation of the efficiency of the species richness assay

Throughout the present analysis, we used sample-based rarefaction curves rescaled to the number of individuals (*sensu* Gotelli and Colwell 2001; see also Longino et al. 2002) to evaluate the efficiency of our survey relative to the sampling effort. Gotelli and Colwell (2001) point out an important distinction between accumulation and rarefaction curves: Sample-based accumulation curves record the total number of species revealed as additional sample units are added to the pool of all previously observed samples. Instead, sample-based rarefaction curves represent the means of repeated re-sampling the pool of N samples at random, and subsequent plotting the average number of species represented by N samples; hence, it is the statistical expectation for the corresponding accumulation curve. The sample order must be randomized when computing species accumulation and rarefaction curves because the order in which samples are added to the totals affects the shape of such curves (see Colwell and Coddington 1994; Gotelli and Colwell 2001 for discussion). Gotelli and Colwell (2001) further emphasize that when sample-based rarefaction curves are used to compare taxon richness at comparable levels of sampling effort, the number of taxa should be plotted, as a function of the accumulated number of individuals, not accumulated number of samples, because datasets may differ systematically in the mean number of individuals per sample.

In the present analysis, we use EstimateS (Colwell 2000) to compute sample-based rarefaction curves, using 1000 random reordering of the samples. We rescaled the expected average number of species to the accumulated number of individuals to compare the efficiency of our survey relative to sample effort. We compare combined-habitat curves to (1) within-habitat curves (i.e. forest- scrub- and steppe-curves), (2) disturbed-habitat and (3) undisturbed-habitat curves based on different subdivisions of our dataset (see Table 1). Note, however, that we do not evaluate the effect of disturbance on sampling efficiency separately within each habitat type (cf. Farji-Brener et al. 2002). If sample sizes are not sufficient, rarefaction will not distinguish between different richness patterns (see Gotelli and Colwell 2001). Hence, throughout the present analysis, all comparisons between disturbed-habitat curves and undisturbed-habitat curves refer exclusively to samples from the three major habitats taken together.

Estimation of species richness by extrapolation

We use EstimateS (Colwell 2000) to compute several extrapolation indices based on different subsets of data, as detailed in Table 2. We compare the species richness estimations coming from several non-parametric extrapolation indices (Chao_1, Chao_2, Jack_1, Jack_2, and ICE) as well as from the asymptotic Michaelis–Menten richness estimator (MMMean) (see Colwell and Coddington 1994, for formal definition). Rosenzweig et al. (2003) conceptually clarifies differences between these two types of indices. Non-parametric indices were designed to overcome sample-size inadequacies and to reveal how many species are present in habitats actually sampled. Hence, they operate only on the results obtained from a particular subset of the total data set and do not represent an extrapolation in strict sense. In contrast, MMMean extrapolates species diversity to the asymptote of the species accumulation curve, thus estimating the number of species in an infinitely large sample (see Rosenzweig et al. 2003; for review: Colwell and Coddington 1994; Gotelli and Colwell 2001).

Given that non-parametric estimations of species richness can be affected by the spatial autocorrelation of data (see Rosenzweig et al. 2003), we use Ws2m (Turner et al. 2000) to compute two additional estimators of species richness, named F5 and $\text{MMMean}_{(\text{shuff})}$ F5 belongs to a family of formulas recently designed for species richness extrapolation (see Rosenzweig et al. 2003 for formal description), which makes no assumptions except that (1) when a

Table 1. Summary of key comparisons and results. Sample-based rarefaction curves are used to compare species richness patterns in different subdivisions of data (see Figure 2).

Datasets	Regional Habitat Heterogeneity					Fire Disturbance		
	Combined-habitat rarefaction curves (Hc)	Within-habitat rarefaction curves (Hw)				Disturbed-habitat rarefaction curves (Hd)	Undisturbed-habitat rarefaction curves (Hu)	
	Individuals	Individuals			Efficiency	Individuals	Individuals	Efficiency
		Fo	Sc	St				
All Beetles	8203	5510	1542	657	Hc, Sc > Fo > St	4551	3607	Hc,Hu > Hd
Carabidae	4432	2688	1201	194	Hc > Fo > Sc > St	2181	2248	Hc, Hd > Hu
Curculionidae	158	89	41	44	Hc > Fo > Sc, St	65	100	Hc, Hu > Hd
Staphylinidae	677	289	378	0	Hc, Fo > Sc	140	568	Hc > Hd, Hu
Ants	109991	1335	15543	92831	Hc > Fo > Sc > St	48013	61664	Hc,Hu > Hd

For each subset of data, combined-habitat curves were compared to within-habitat curves and disturbed-habitat curves to undisturbed-habitat curves. Individuals: averaged accumulated number of individuals after 1000 random reorderings of samples. To see actual number of individuals captured see Table 2. Fo = Forest, Sc = scrub, St = Steppe.

sample contains only one individual the formula tells us that it contains one species, and (2) species richness rises monotonically toward an asymptote. F5 has been reported to be the most successful estimator when information is least complete (Rosenzweig et al. 2003). It performs well when individuals are shuffled or sample order is shuffled for many (more than 10) runs (Turner et al. 2000). In the present analysis we shuffle sample order and individuals over 50 runs to obtain F5 estimations. We estimated MMMean$_{(shuff)}$ using Ws2m and the same shuffling criteria.

Table 2. Number of species estimated by extrapolation, and performance of different estimators.

Taxon	Estimator	S_{obs}(Ns)	Ni	SR	$r_s(p)$	MD	MSD
All Beetles		177 (38)	8203				
$z_s = 179$	**Chao1**			**239.30 ± 21.76**	**1.00 (< 0.0001)**	**55.78**	**2.29**
$z_i = 8244$	Chao2			290 ± 34.44	0.98 (< 0.0001)	101.98	1.81
	Jack1			255.87 ± 12.80	1.00 (< 0.0001)	57.66	9.08
	Jack2			305.87	1.00 (< 0.0001)	93.66	0.65
	ICE			292.70	0.87 (< 0.0001)	105.63	3.13
	MMMean			229.98	0.99 (< 0.0001)	73.44	55.45
	MMMean$_{(shuff)}$			178.89	Equal than z_s		
	F5			179.69	Equal than z_s		
Carabidae		22 (36)	4432				
$z_s = 22$	**Chao1**			**30 ± 11.66**	1.00 (< 0.0001)	**3.45**	**15.58**
$z_i = 4435$	Chao2			70.70 ± 59.28	0.84 (< 0.0001)	19.21	593.52
	Jack1			32.69 ± 3.64	1.00 (< 0.0001)	6.33	46.15
	Jack2			43.08	1.00 (< 0.0001)	11.16	155.14
	ICE			51.29 ± 0.04	0.99 (< 0.0001)	10.44	164.14
	MMMean			23.43	0.87 (< 0.0001)	4.38	29.99
	MMMean$_{(shuff)}$			21.09	Lower than z_s		
	F5			22.45	Equal than z_s		
Curculionidae		23 (28)	123				
$z_s = 23$	Chao1			27.50 ± 4.8	0.79 (< 0.0001)	7.54	68.58
$z_i = 123$	**Chao2**			27 ± 3.74	**0.29 (0.14)**	14.75	260.06
	Jack1			30.71 ± 2.73	0.99 (< 0.0001)	**7.39**	**59.93**
	Jack2			30.99	0.78 (< 0.0001)	10.72	131.43
	ICE			31.75	0.74 (0.0001)	13.47	198.80
	MMMean			31.50	0.99 (< 0.0001)	9.10	88.80
	MMMean$_{(shuff)}$			20.43	Lower than z		
	F5			19.99	Lower than z		
Staphylinidae		36 (24)	667				
$z_s = 36$	Chao1			55.60 ± 14.36	0.99 (< 0.0001)	16.17	289.83
$z_i = 667$	Chao2			72.10 ± 23.90	0.84 (< 0.0001)	31.80	1082.13
	Jack1			**54.21 ± 5.87**	**1.00 (< 0.0001)**	**12.64**	**182.56**
	Jack2			67.24	1.00 (< 0.0001)	20.71	504.93
	ICE			67.21 ± 2.82	0.81 (< 0.0001)	33.24	1188.81
	MMMean			53.68	1.00 (< 0.0001)	19.95	428
	MMMean$_{(shuff)}$			36.54	Equal than z		
	F5			**39.67**	**0.99 (< 0.0001)**	**9.30**	**97.63**

Table 2. (Continued)

Taxon	Estimator	S_{obs}(Ns)	Ni	SR	$r_s(p)$	MD	MSD
Ants		21(38)	109991				
z_s = 21	Chao1			22 ± 3.74	0.51(0.002)	−0.94	35.30
z_i = 115056	Chao2			29 ± 11.66	0.91 (< 0.001)	5.79	41.51
	Jack1			**24.89 ± 1.87**	0.99(< 0.0001)	**4.08**	**17.42**
	Jack2			22.76	0.99 (< 0.0001)	5.65	35.28
	ICE			23.33 ± 0.01	0.60 (0.0003)	4.37	34.70
	MMMean			23.39	0.78 (< 0.0001)	5.27	39.02
	MMMean$_{(shuff)}$			**26.86**	**0.38 (0.02)**	8.39	95.10
	F5			21.081	Equal than z		

z_s = actual number of species captured, z_i = actual number of individuals captured. S_{obs} = average number of species observed after 1000 random reorderings of samples. Ns = number of samples. Ni = average number of accumulated individuals after 1000 random reorderings of samples. SR = estimated mean species richness ± one standard deviation of the mean; estimations are the averages of results at the last step (the one with the largest number of accumulated individuals); r_s = Spearman Rank Correlation Coefficient of each estimator v. the number of accumulated individuals. p = error probabilities. MD = Mean Deviation, MSD = Mean square deviation. The best species richness estimation/s for each data set is/are in bold.

As already stated in the Introduction, if a species richness estimator tends to converge with the observed species richness and it is independent of sample size or the number of individuals, it is more likely to be a reliable estimate of total species richness for any given region (e.g., Colwell and Coddington 1994; Gotelli and Colwell 2001). We apply Spearman Rank Correlation Coefficients (r_s) to test for an association between the different species richness estimations and the number of accumulated individuals (= sample effort). We compute mean deviation (MD) and mean square deviation (MSD) (see Palmer 1990, for formal definitions) to evaluate the extent to which different indices tend to converge with the observed species richness. Mean deviation (MD: see Palmer 1990) is a measure of bias. It is positive when a species richness estimator overestimates and negative if it underestimates. Mean square deviation (MSD: see Palmer 1990 for formal definition) measures the estimator's closeness to the observed (S_{obs}) species richness after 1000 random reorderings of samples. Estimators with small MSDs tend to converge with S_{obs} and, hence, are preferred to those with large MSDs. Throughout the present analysis we define as "best" estimators for each data set those with small MD, MSDs and/or r_s.

Evaluation of the completeness of the species richness assay

The proportion of total estimated species richness that was measured in pitfall samples was used as an index of completeness. For some non-parametric estimators (e.g., ICE) the estimated species richness will approach the observed richness (i.e. completeness) when the number of rare species declines to an estimate-specific level (Fisher 1999). Thus, we examined whether the number of rare species tend to decrease, increase or maintain constant with increased sampling, as an additional way to evaluate the completeness. We used

EstimateS (Colwell 2000) to compute sample-based rare species accumulation curves for the different subsets of data (as detailed in Table 1) relative to sample effort. As above, we used 1000 random reorderings of samples and rescaled the results to the number of accumulated individuals to standarized sample effort. We consider the number of singletons (i.e. species with only one individual) and uniques (i.e. species that occur in only one sample) in the pooled *N* samples alternatively as two different expressions of rarity.

Finally, we compare our species richness estimations with the currently 'known' number of species, as defined by historical records reported by professional taxonomists in southern South America. Such information is only available for three taxa (Carabidae, Staphylinidae and ants) and come up from different geographic scales and sources of data. For the Carabidae, we use the list of georreferenced collection localities for species in Chile and Argentina compiled by S. Roig-Juñent (personal communication). The number of species reported for collection localities between latitudes: 41°–41°30′ S and longitudes: 71°–71°40′ W is the 'known' species richness for the Carabidae within our study region. For Staphylinidae, the 'known' fauna is the number of species listed for Rio Negro Province (Argentina) by Newton and Thayer (2003). For ants, it is the list of species reported for NW Patagonia by Kusnezov (1953, 1959) and the number of species recorded as present in both Neuquén and Rio Negro by Cuezzo (1998).

Results

We captured a total of 8244 individuals of beetles representing 179 RTUs. About 40% ($N = 71$) of these RTUs were identified as known species by professional taxonomists, and the rest of the material was sorted out to morphospecies within known genera (32%; $N = 58$) or families (28%; $N = 50$). We captured a total of 115056 individuals of ants, which were all sorted out to species level (100%). Note, however, that species and morphospecies are used equally in all subsequent analyses. Table 1 shows a summary of key comparisons and results presented in detail below.

Test of the effect of regional habitat heterogeneity on sampling efficiency

After re-scaling to the accumulated number of individuals, the combined-habitat curves are in general steeper than the within-habitat curves. This indicates turnover of species among habitats. However, there are clear differences between these two major taxa. The evident separation between the combined- and within-habitat curves for ants (Figure 2) suggests that sampling over the three habitats is necessary to capture the total species richness of ants at regional scale. In contrast, all beetles analyzed together suggest that, sampling in the scrub may be as efficient as sampling over the three major habitats.

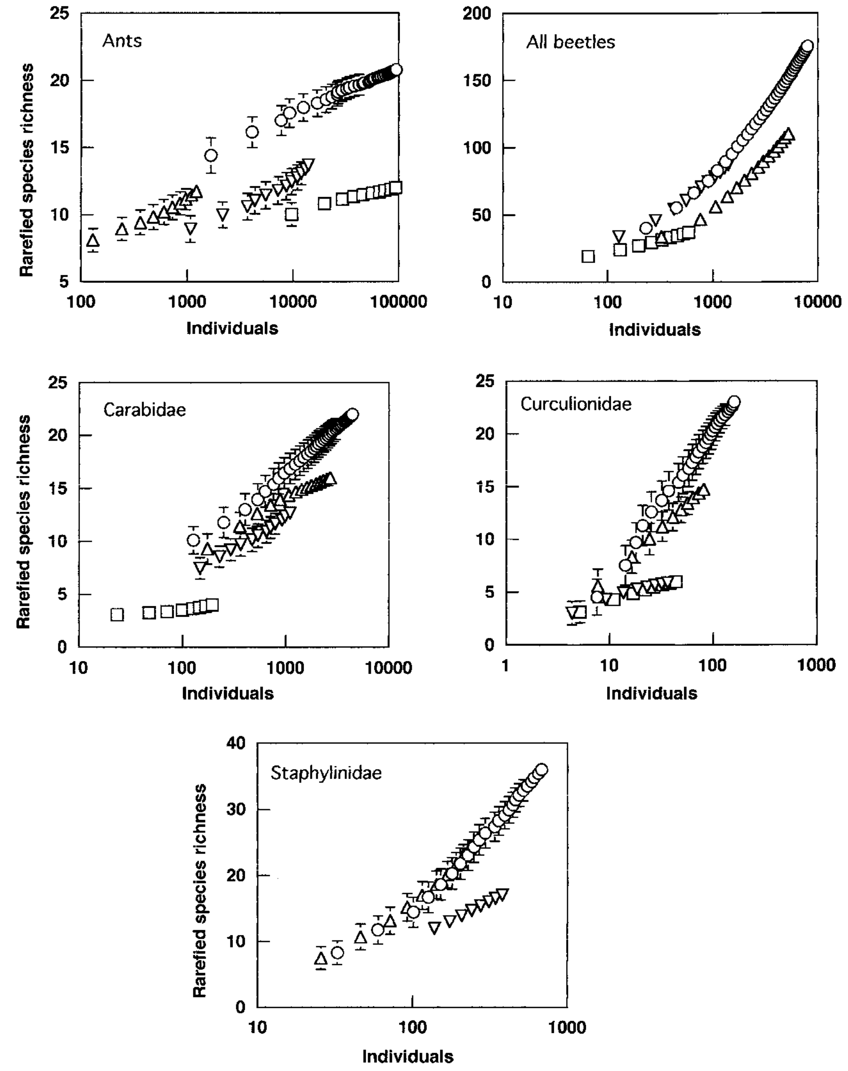

Figure 2. Sample-based rarefaction curves rescaled to individuals used to compare the efficiency of the species richness assay over the whole study region and within three major habitats considered. Combined-habitat rarefaction curves are compared to within-habitat rarefaction curves for the different subsets of data, as detailed in Table 1. Circles are used for combined-habitat curves, triangles for forest-, inverted triangles for scrub-, and squares for steppe-curves. Error bars correspond to one standard deviation of the mean after randomization.

Indeed, the combined-habitat rarefaction curve overlaps the within-scrub rarefaction curve for this dataset (Figure 2). Sampling exclusively in the forest is less efficient. Although this strategy may result in a similar rate of accrual of new beetle species per unit of effort (i.e. the within-forest rarefaction curve parallels the combined-habitat rarefaction curve), the absolute number (= total richness) of species captured in the forest is lower than the number recorded either in the scrub or over the three habitats (Figure 2).

The separate analysis of the three most diverse families of beetles: Carabidae, Curculionidae, Staphylinidae, each with more than 20 species, shows that the effect of habitat heterogeneity on sampling efficiency depends on sampling effort. Visual inspection of curves (Figure 2) suggests that it is only above certain numbers of individuals captured (Carabidae: 1000; Curculionidae: 100; Staphylinidae: 300) that the differences between combined-habitat and within-habitat sampled based rarefaction curves emerge.

Within-habitat sample based rarefaction curves show consistent differences among habitats. Ants, Carabidae, Curculionidae and Staphylinidae suggest that it is more efficient sampling in the forest rather than in the other two habitats, both in terms of the rate of accrual of new species as well as the total number of species captured (Figure 2). As discussed above, all beetles taken together do not show the same trend, which would suggest that neither of these three beetle families (Carabidae, Curculionidae, Staphylinidae) might be taken with confidence as surrogate taxa for all beetles.

Test of the effect of disturbance on sampling efficiency

Both ants and all beetles taken together show that the strategy of sampling in both disturbed and undisturbed habitats may increase the efficiency of the species richness assay, compared to the strategy of sampling exclusively in undisturbed habitats (Figure 3). However, sampling exclusively in disturbed habitats is indeed less efficient. The number of new species captured relative to sampling effort tends to decrease significantly in disturbed habitats, and more strongly for ants at higher levels of sampling effort (Figure 3). These patterns are not universal, and the three families of beetles (Carabidae, Curculionidae, Staphylinidae) analyzed separately show idiosyncratic trends. Although Curculionidae does show the same pattern that all beetles taken together, the other two families differ. Staphylinidae suggests the positive effect of taking into account both types of habitats for an efficient design of sampling strategy (Figure 3). Although the number and abundance of Staphylinidae species are significantly lower in disturbed habitats as compared to undisturbed ones, sampling either in exclusively disturbed or undisturbed habitats results in a significantly lower number of species captured per unit of effort (Figure 3). In contrast, Carabidae shows an opposite trend, suggesting that sampling in disturbed habitats is an efficient strategy to increase the rate of new species accrual as well the total number of species captured relative to sample effort (Figure 3).

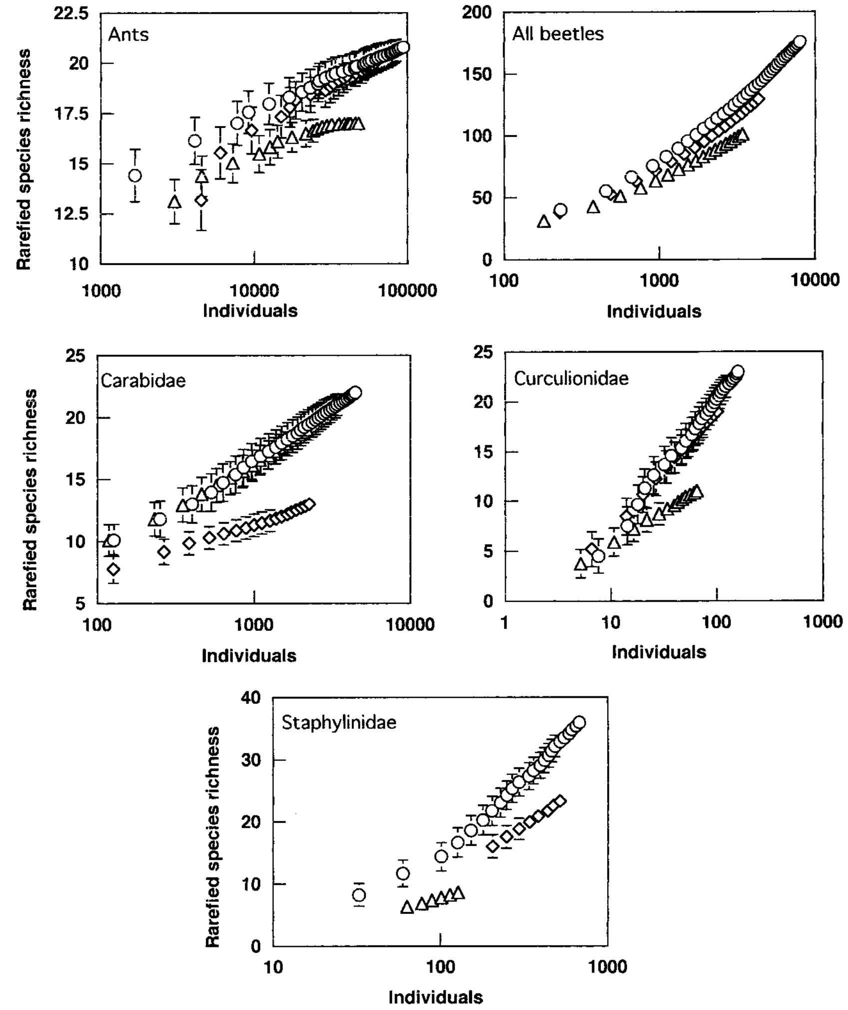

Figure 3. Sample-based rarefaction curves rescaled to individuals used to compare the efficiency of the species richness assay in burned and unburned habitats within the study region. Disturbed-habitat rarefaction curves are compared to undisturbed-habitat rarefaction curves for different subsets of data, as detailed in Table 1. Circles are used for combined-habitat curves, triangles for burned-habitat- and diamonds for pristine-habitat-curves. Error bars correspond to one standard deviation of the mean after randomization.

Estimation of species richness by extrapolation and evaluation of completeness

Most non-parametric estimators (except Chao1 for ants: see Table 2) tended to overestimate species richness as compared to S_{obs}. In contrast, after shuffling the number of individuals among samples over each run, F5 performed well only for the Staphylinidae and so did $\mathrm{MMMean}_{(\mathrm{shuff})}$ for ants. For the remaining datasets these two estimators were not useful for species richness extrapolation because they resulted in values of estimated species richness lower or equal than the actual number of species (Table 2). The lower values of MD and MSD obtained for Jack_1 (Curculionidae, Staphylinidae, ants: Table 2) and Chao_1 (Carabidae: Table 2) suggest that these non-parametric estimators tend to converge with S_{obs} and may perform better than the others for these subsets of data.

Overall, we captured between 70% and 90% of the estimated species richness for the region studied, which can be taken as preliminary indication of the completeness of our species richness assay (Table 2). All estimators are highly correlated with the number of accumulated individuals; the only exception is Chao_2 estimator for Curculionidae (Table 2). The positive relationship between sampling size and estimated species richness is explained by the increase in the number of new rare species (singletons and uniques) collected with increasing sampling effort (Figure 4); see also Longino and Colwell 1997; Fisher 1999).

An alternative approach to evaluate the level of completeness is to compare the observed and the best species richness estimations with historical records of the number of species reported for the region studied. According to this criterium, our species richness assay effectively captured a reasonable proportion (>50%) of carabid, staphylinid and ant species known. Kusnezov (1953) reported that the ant fauna of Lanín and Nahuel Huapi National Parks is composed by 21 ant species, which corresponds closely with the number of species observed in the present study (Table 2). We captured 9 out of the total of 10 ant genera reported by Kusnezov (1953, 1959) for western Patagonia. Based on the list of species by Cuezzo (1998), a total of 26 ant species inhabit both Rio Negro and Neuquén, which approaches the number we estimated by extrapolation (Table 2). On the other hand, our study captured about 60% of Carabidae species known for the region based on a total of 36 species reported in Roig-Juñent's database, between latitudes: 41°–41°30′ S and longitudes: 71°–71°40′ W. The known number of species ($N = 36$) is well within the range of species richness estimated by Chao_1 (see Table 2). We captured 36 out of 67 (53.7%) species of Staphylinidae listed by Newton and Thayer (2003) for Rio Negro Province. The number of staphylinid species estimated by Jack_1 (54.21 ± 5.87) tends to approach to the total known.

Discussion

The present study provides useful information to evaluate the efficiency of different strategies, i.e. how to apportion sampling effort among habitat types using pitfall traps, to capture a great number of beetle and ant species in rapid diversity assessments within the Nahuel Huapi region. This may be of primary importance in regions like northern Patagonia whose arthropod fauna is

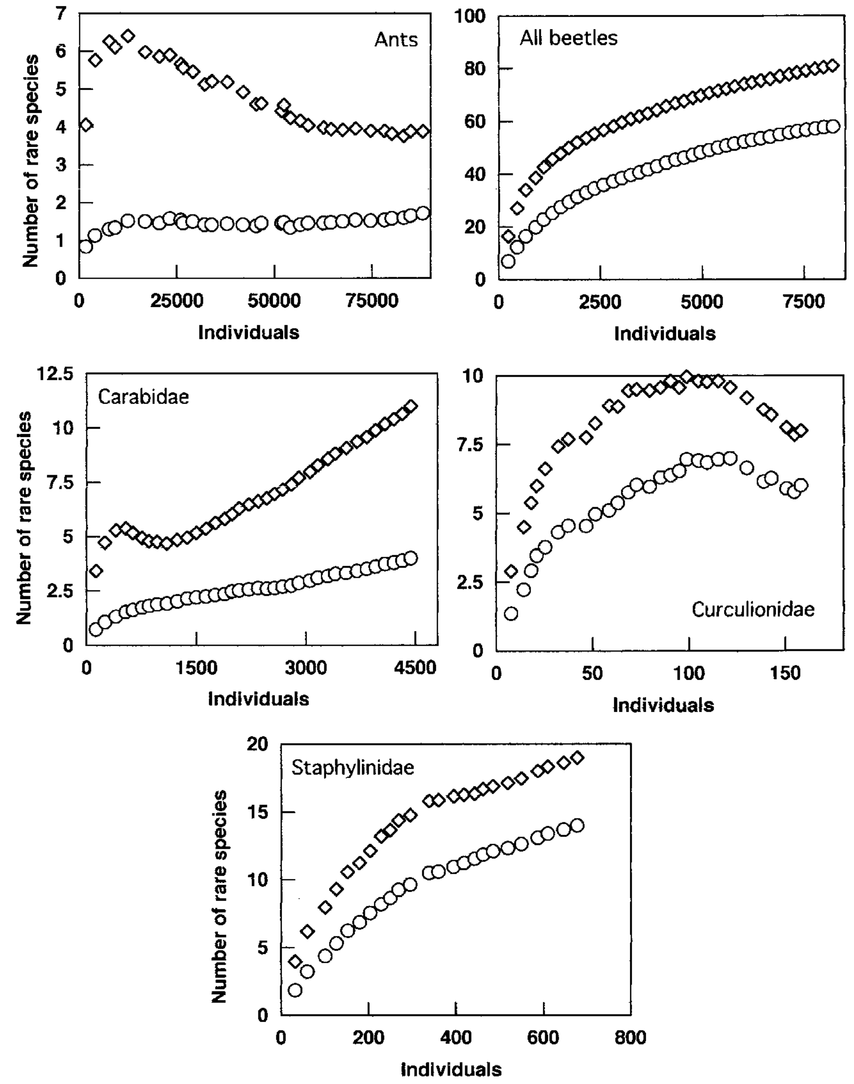

Figure 4. Rare species (circles: singletons; diamonds: uniques) sampled-based accumulation curves rescaled to individuals used to estimate the completeness of the species richness assay. Error bars correspond to one standard deviation of the mean after randomization.

poorly known. In particular, the insect fauna of the temperate rainforests in Argentina is largely un-surveyed (Morrone and Coscarón 1998, Mario Elgueta, MNHN Santiago, personal communication). Thus, this increases the interest in the trade-off between survey cost and the ability to record the highest species richness irrespective of species identity. Moreover, given a situation where budget restrictions limit the possibility of sampling to only one season and to a relatively small number of collection stations, the application of sample based rarefaction curves allows comparing the efficiency of different sampling strategies (i.e., sampling in only one habitat vs. over different habitats; in natural habitats vs. in disturbed habitats).

Sample based rarefaction curves, as applied in the present analysis, clearly show that the high regional habitat heterogeneity along the west-to-east gradient is paralleled by a turnover of beetle and ant species. As a consequence, spatial stratification of sampling over the three major habitats (forests, scrub and steppe) may represent an adequate strategy to improve sampling efficiency of beetles and ants within the region studied. However, within the studied region, this kind of sampling stratification is only meaningful after certain threshold levels of sampling efforts (e.g., Carabidae = 1000 individuals, see Figure 2). At lower levels of sampling effort, the number of new species captured per unit of effort (i.e. accumulated number of individuals) tends to converge regardless of the sampling strategy (see Figure 2).

Sample based rarefaction curves also show that beetles and ants may show distinct patterns in species diversity. As previously found in other regions of the world (e.g., for ants, beetles and spiders in Australia: Oliver and Beattie 1996a), trends in species richness observed in ants may not indicate similar trends in beetles. This cautions against using ants and beetles as 'surrogate taxa' for each other (*sensu* Hammond 1994), for species richness estimations or evaluation of ecological theory. Instead, we suggest that both taxa should be considered 'focal', as they may offer complementary information for the analysis of the effect of disturbance and regional habitat heterogeneity on species diversity patterns at regional scale.

Ants are good indicators of the west-to-east replacement of habitats that occur at regional scale in NW Patagonia. Sampling over the three habitats is necessary to capture the greatest number of ant species with minimum sampling effort. In this way, our study confirms previous evidence suggesting that ants are responsive to environmental heterogeneity at different spatial scales, from small (e.g., m^2: Kaspari 1993; Farji-Brener et al. 2004), to intermediate (e.g., within habitats: Johnson 1992; Bestelmeyer and Schooley 1999) to large spatial scales (e.g., between habitats: Bestelmeyer and Wiens 2001). In general, ants are well known to reflect the level of habitat disturbance and succession, as well as to be good bio-indicators of the degree of ecosystem condition (Andersen 1997, Vasconcelos 1999; Vasconcelos et al. 2000). However, a priori, there is no clear prediction about the effect of different disturbances on ant diversity; indeed, ant diversity after fire may increase (see Folgarait 1998), decrease (e.g., York 2000) or remain unchanged (e.g., Parr et al. 2004). In the present analysis, we show that, at a high level of sampling effort, the expected rate of new species accumulation is lower in disturbed habitats.

Beetles also show turnover of species along the west-to-east gradient. However, they differ from ants in several aspects. All beetles taken together suggest that sampling in the scrub is equally efficient as sampling over the three habitats. This would suggest that, in contrast to ants, concentration of sampling effort in the scrub might pay back with the same rate of new species accumulation as sampling over the three habitats relative to sample effort. Nonetheless, it is interesting to note that the three better-represented surrogate families of beetles analyzed separately (i.e. Carabidae, Curculionidae, Staphylinidae with more than 20 species recorded in the present study) do not suggest the same trend but the opposite: sampling in the scrub is indeed less efficient than sampling over the three habitats taken together, or even less efficient than sampling exclusively in the forest. Hence, the pattern in all beetles taken together might be the consequence of the scrub harboring species of other less well-represented families of beetles in terms of number of species, though taken together they may contribute significantly to shape overall species richness patterns in the regional pool of beetle species. In this way, our study warns against the use of surrogate families of beetles to infer overall patterns in species diversity of all beetles within the region studied. Also, in terms of future species inventories, researchers should take into account that there is no single strategy that can be applied to optimize the cost of inventories for all beetle families.

In general, our study suggests that an efficient sampling strategy for beetles in NW Patagonia should include both burned and unburned sites of collection. However, we recommend taking into account that the effect of disturbance on sampling efficiency may vary (i.e. be positive or negative) depending on whether all beetles are taken together or, instead, any of the surrogate families are analyzed separately. For instance, there is a negative effect of disturbance on the sampling efficiency of Curculionidae, whereas Carabidae clearly suggest a positive effect. Indeed, carabid beetles suggest that sampling exclusively in burned environments might be as efficient as sampling in burned and unburned environments, i.e. both in terms of the expected number of carabid species and the rate of new carabid species accumulation. Of course, this conclusion is based exclusively on species richness patterns and species accumulation rates, and do not take into account likely differences in species composition between both types of environments, i.e. whether there are some rare species that might be found exclusively in pristine (or disturbed) habitats.

Although community characterization is not the main focus of the present study it is worthwhile to mention that the interplay between biological and non-biological (= sampling) factors may ultimately account for differences in the effects of heterogeneity and disturbance on the sampling efficiency. Pitfall trap catches depend on species' abundance and activity. It is well documented that this sampling method is more efficient to capture mobile epigaeic insects than less mobile or smaller species (Luff 1975; Spence and Niemelä 1994; Melbourne 1999). Thus, one of the reasons why our richness assay captured a high proportion of the historically known fauna of ant and carabid species within the region may be related to the high mobility of these insect taxa. On the other hand, the efficiency of pitfall traps depends on vegetation density (e.g., Melbourne 1999), but also does the structure of epigaeic insect communities. Comparative and experimental evidence suggests patterns in the abundance and diversity of omnivorous, detritivorous and carnivorous coleopteran species may indeed change substantially along the west-to-east gradient in response to micro-scaled environmental changes in vegetation cover (Mazía 2004). It is also likely that the effect of fire affected distinct taxonomic groups differently. For instance, in the southern Swiss Alps, Moretti et al. (2004) found that the species richness of Carabidae (and also spiders) may increase at sites burned repeatedly, in contrast to Curculionidae or ants. These differences, which are quite consistent with the results reported in the present study, suggest that those predator taxa could increase quickly after being reduced by fire by profiting from abundant food in the post-fire mosaic of ground habitats (see Moretti et al. 2004 and other references therein). However, the effect of rapid increase in abundance on sampling efficiency might be enhanced by a 'sampling effect' if greater mobility of beetles occurred in those environments with ongoing processes of natural regeneration, mainly due to quick searches for food, short times of permanence in vegetation patches and frequent dispersal (see e.g., Price 1992).

Finally, critical evaluation of our species richness assay allows detecting those aspects that may require careful consideration for future ecological analyses within the same area of study. One issue is related to the question of whether it is necessary to increase the sampling effort for obtaining more reliable species richness estimations. Although, in the present analysis, non-parametric estimators of regional species richness reported 'reasonable numbers' of species as compared to historical records, all estimations were highly correlated to sample effort. The level of completeness, as expressed by the percentage sampled of the total species richness estimated, may be rather unreliable when richness estimations are not independent of sample size because most non-parametric estimators assumed that the number of rare species decreases with sampling effort (Fisher 1999). Nonetheless, given that using a single trapping method, i.e. pitfall traps in the present analysis, makes the potential sampling universe much smaller than the absolute regional species pool, it is difficult to obtain richness estimations independent of sampling effort. Thus, the levels of completeness reported in the present analysis may be rather overestimated, and our estimations should be viewed only as minimum estimates of species richness (see Longino et al. 2002).

In conclusion, the present analysis suggests that future species inventories within the region would benefit from assuming a regional perspective that take into account how the effect of several environmental variables – habitat structure, disturbance – may interact at a geographic scale with the presence of different taxa. Given that there is no single sampling strategy that can be best for all taxa at all sites, sampling stratification over the three major habitats while including pristine and disturbed sites can be the best strategy to obtain high numbers of beetle and ant species in rapid, short-term species richness assays. This can be view as starting point for future conservation planning in northern Patagonia.

Acknowledgments

We deeply thank those professional taxonomists that generously devoted their time to species determination, namely: Sergio Roig-Juñent (Carabidae, Chrysomelidae and Bruchidae), Gustavo Flores (Tenebrionidae), Federico Ocampo (Scarabaeidae, Trogidae, Geotrupidae and Lucanidae), Vladimir Gusarov (Staphylinidae), Paula Posadas (Curculionidae), Mario Elgueta (Mordellidae, Leiodidae, Coccinellidae, Nitidulidae), and Fabiana Cuezzo (Formicidae). S. Roig-Juñent also shared with us his georreferenced database on Carabidae. Juan and Joaquina Sackmann did Figure 1 and Monica de Torres Curth provided photographs. Insightful comments by two anonymous reviewers improved the manuscript. This work is part of a project funded by Agencia/Foncyt (BID 1201/OC-AR-PICT No. 01-11826), CONICET and Universidad Nacional del Comahue.

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