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The value of timber quality forests for insect conservation on Tierra del Fuego Island compared to associated non-timber quality stands

María Vanessa Lencinas · Guillermo Martínez Pastur · Christopher B. Anderson · Carlos Busso

Abstract Insect community studies related to forest management focus principally on timber-quality stands, and often omit the remainder of the landscape. This study aimed mainly to compare insect communities of primary timber-quality forests (*Nothofagus pumilio*) with associated non-timber-quality stands (wetland, edge, riparian and *N. antarctica* forests), and secondarily to characterize these insect assemblages throughout the growing season and at different vertical strata to evaluate the importance of each habitat type for insect conservation. A total of 18,800 individuals belonging to 231 RTUs (recognizable taxonomic units) were identified, of which Diptera, Hymenoptera, Lepidoptera and Coleoptera were the dominant orders. Lepidoptera RTUs were mostly generalists, while the other main orders were most frequently found in timber-quality forests and included many RTUs with specific environmental requirements. Timber-quality stands had higher richness and abundance than associated non-timber-quality forests and possessed more exclusive species (18%), while 39% of RTUs were shared between all sites. The spatial heterogeneity of timber-quality stands generated different niches and favored insect diversity, which would not have been maintained by protecting non-timber-quality stands alone. Consequently, the proper management of subantarctic *Nothofagus* forests must include the conservation of timber-quality stands, as protection of non-timber-quality areas alone will not be sufficient for insect conservation at the landscape scale.

Keywords Diversity · Forest management · Sustainability · *Nothofagus* · South Patagonia

Introduction

Forested landscapes consist of a mosaic that includes different site types. Within this mosaic, timber-quality stands rarely constitute continuous extensions because they are mixed with associated non-timber-quality stands. While timber forests occupy the best site quality areas and yield commercial wood products, the associated non-timber-quality stands include forests which cannot be harvested because they are not profitable, have legal restrictions, or ensure especially protective ecosystem functions (Lencinas et al. 2005). These associated stands are considered non-timber-quality sites for a variety of reasons related with low site quality due to: (a) soil impediments; (b) excess water or wind exposure; (c) containing noncommercial tree species; (d) bordering streams; (e) abutting roads, range-lands or peat bogs; and (f) having excessive slopes.

Silvicultural management applied in timber-quality stands (e.g., regeneration cuts or thinnings) modifies

M. V. Lencinas (✉) · G. Martínez Pastur
Centro Austral de Investigaciones Científicas (CONICET),
CADIC, cc 92, 9410 Ushuaia, Tierra del Fuego, Argentina
e-mail: vlencinas@gmx.net

C. B. Anderson
Omora Ethnobotanical Park, University of Magallanes, Puerto
Williams, Chile

C. B. Anderson
Institute of Ecology and Biodiversity, Casilla 653, Santiago,
Chile

C. Busso
Centro de Recursos Naturales Renovables de la Zona Semiárida
(CONICET), Bahía Blanca, Argentina

C. Busso
Departamento de Agronomía, Universidad Nacional del Sur,
Bahía Blanca, Argentina

biodiversity, altering assemblage or producing species losses (Deferrari et al. 2001; Jalonen and Vanha-Majamaa 2001; Spagarino et al. 2001; Martínez Pastur et al. 2002), due to changes in microclimatic conditions, nutrient cycles or forest structure (Reader and Bricker 1992; Lewis and Whitfield 1999; Caldentey et al. 2001, 2005a, b). Most studies, however, have only analyzed biodiversity loss in the timber-quality stands alone (Quinby 2000; Deferrari et al. 2001; Spagarino et al. 2001; Jalonen and Vanha-Majamaa 2001; Martínez Pastur et al. 2002) without considering the interaction with the remainder of the landscape, which includes associated non-timber-quality stands (Hutchinson et al. 1999; Rosso et al. 2000).

Arthropods in forest ecosystems are widely recognized to play a key role in ecosystem processes. For example, insects and arachnids are frequently used to evaluate the effects of human activities on biodiversity and environment quality (Kim 1993; Niemelä 2001). These groups are good indicators at the landscape level (Lewis and Whitfield 1999) as well, because their abundance, species richness, and occurrence are sensitive to local resource variations (Werner and Raffa 2000). Boreal forest insect communities are rather well-known (Martikainen et al. 2000; Niemelä 2001), in contrast to the austral forest ecosystems of the Tierra del Fuego and Cape Horn Archipelagos (Lanfranco 1977; Stary 1994; Spagarino et al. 2001). However, few works in both hemispheres have defined ecological characteristics or relationships between timber-quality and associated non-timber-quality stands (Giganti et al. 1994). Improving our knowledge of insects in the context of forest management in this respect is necessary for effective arthropod conservation (Kim 1993), but most studies have only analyzed timber-quality forest insect diversity. In this way, generalist species have little importance for conservation strategy designs, while those species with specific environmental requirements acquire greater conservation importance.

The aims of this work were to rectify this problem for the world's most austral temperate forests on Tierra del Fuego Island by: (1) comparing *Nothofagus* forest insect communities, including richness and abundance across different forest site types; (2) characterizing these community parameters in two seasonal periods and three vertical strata; and (3) using this information to evaluate the importance of timber-quality versus non-timber-quality stands for insect conservation in the subantarctic landscape.

Methods

Location of the study area and stand characterization

Temperate timber-quality forests and their associated non-timber-quality stands were selected in the central part of the Argentine portion of Tierra del Fuego Island, within a *Nothofagus* forest at Ushuaia Ranch (54°27′32″ S, 67°30′16″ W). The study site was located 10 km north of Fagnano Lake and 5 km east of Yehuin Lake. Climate is characterized by short, cool summers and long, snowy and frozen winters. Mean monthly temperatures vary from about –7°C to 14°C. Absolute temperatures range from –17°C in July to 22°C in January. The growing season extends for about 5 months, and only 3 months per year are frost-free. Precipitation is near 400 mm per year, and average wind speed is 8 km h^{-1}, reaching up to 100 km h^{-1} during storms (Lencinas et al. 2005).

An area of 1,000 ha was chosen (20% of the ranch). At the site, no intensive cattle grazing had occurred within the past 10 years. However, natural foraging pressure from guanaco (*Lama guanicoe* Müller) did exist throughout the study area (Pulido et al. 2000). Analysis of aerial photos (*Instituto Geográfico Militar*, February 1989, 1:20,600) or satellite images (SPOT, February 1995) and ground truthing with field site visits allowed us to classify forests into six clearly distinct site types: (a) two sites of *N. pumilio* forests, one on flat ground (*LF*) and one a south-facing hillside (slope of 25°) (*MHLF*) with timber-quality stands of commercially productive value; and (b) four associated non-timber-quality site types. The non-timber-quality forests were: (i) edges between timber-quality forests and rangeland (*BLR*), (ii) *N. antarctica* (Forster f.) Oersted forests (*ÑF*), (iii) forested wetlands (*W*), and (iv) riparian forests (*S*). The timber-quality forest sites had: (1) at least a site quality *V* (Martínez Pastur et al. 1997), (2) no harvest restrictions established in the provincial forest law #145 and (3) could potentially be harvested for timber volumes of up to 40 m^3 ha^{-1} (healthy logs up to 30 cm diameter and 3 m long). Associated non-timber-quality stands were forests where logging activities could not be carried out because: (a) dominant trees were not commercial species, such as *N. antarctica*, (b) flooded forest floors excluded traffic of heavy machinery, such as wetlands, and (c) forest edges (*BLR* and *S*) that serve special protection functions against wind and water erosion. A more detailed site type description is given in Lencinas et al. (2005). Stands representing the described site types were selected for sampling along a north–south topographic gradient, and each site type was 200–1,000 m apart. All stands presented a good conservation status and had easy field access.

Forest structure was characterized with biometric variables (basal area, diameter at breast height, tree density, dominant tree species, dominant height, total over bark volume, crown cover and site quality), which were previously reported in Lencinas et al. (2005). Timber stands represented 64% of the study area and had larger trees (up to 23 m height) with a closed canopy (up to 96% plant cover) and high tree over bark total volume (600–700 m^3 ha^{-1}). Meanwhile, edge

sites and riparian stands had a similar forest structure to the timber-quality stands, but occupied only 2% and 8% of the area, respectively. In contrast, *N. antarctica* forests represented 11% of the area and had lower height, crown cover and volume (55%) than timber-quality forests. Finally forested wetlands, where timber-quality and non-timber-quality species coexisted, covered 2% of the area and presented lower crown cover (77%). The remaining 13% of the area corresponded to open clearings, including rangelands and peat bogs (12% and 1% respectively).

Insect sampling methodology

Adult mobile epigean individuals of the Insecta class (except Collembola) were collected at the beginning (November 1998) and end (March 1999) of one growing season, which corresponds to a relevant period for insect thermal activity that goes from November to April on Tierra del Fuego (Niemelä 1990). Sampling was done using a wide spectrum trap system with 13 traps randomly distributed near the geographic center of stands. To collect insects at the level of leaf litter, the trap system included one pit-fall trap (100×15×8 cm) (Barber 1931). To collect insects at the understory (0.20–1.00 m height) and canopy levels (3/4 total height of overstory, which was 10–13 m for *N. antarctica* forests and 16–20 m for *N. pumilio* stands), the trapping included smell ethanol attractive traps (20 cm diameter), black and white cold fluorescent light traps (20 cm diameter with 4 watt lamps) (Barratt et al. 1972) and color attractive trays (10 × 10 × 5 cm, using yellow, white and sky-blue colors), one at each vertical sampling stratum. Water was used as a retention agent and formaldehyde as a preservative. Commercial detergent was employed to diminish surface tension. Two stands of each site type were sampled during a 24 h sampling period ($n = 2$ collections per site type, at each growing season sampling time). This period was demonstrated to be appropriate for insect communities in *Nothofagus* forests (Spagarino et al. 2001). Collections were carried out under equivalent climatic conditions, discarding days of strong winds or heavy rain.

After trapping, individuals were quantified and classified under a binocular dissecting scope (×10–×20) to order and family levels (except for Lepidoptera and Psocoptera), following the classification proposed by Richards and Davies (1984) and Romoser and Stoffolano (1998). Because Patagonian insect systematics is still incomplete, either the recognizable taxonomic unit (RTU) or the morphospecies concept was utilized (Oliver and Beattie 1993). The use of RTUs instead of formal taxonomic species may be sufficiently close to estimate species richness with average errors below 15% in rapid assessment of biodiversity inventories, monitoring or preliminary ecological studies (Oliver and Beattie 1993). Likewise,

RTUs have been demonstrated to be a good tool for insect diversity studies in *Nothofagus* forests (Spagarino et al. 2001). The RTUs were deposited in the permanent reference collection at *Centro Austral de Investigaciones Científicas* (*CADIC-CONICET*) in Ushuaia, Argentina.

Data analysis

Recognizable taxonomic unit's rarity was analyzed (Willott 2001; Novotný and Basset 2000) as ''very common species'' (more than 1% of the total captures), ''common'' (between 0.05% and 1%), ''rare'' (less than 10 captures), and ''singleton.'' Singletons were classified at local (considering each habitat type) or regional (considering the whole forest landscape) scales. A dominance index (*DI*) was used to evaluate importance at the order or family level, relating abundance within each site (a_i) to the total number of captures (A) by the equation: $DI = (a_i * 100) A^{-1}$ (Saiz and Zalazar 1982).

Comparisons of richness and abundance among the six site types, two seasons and two vertical strata were done with a three-way analysis of variance ($n = 2$; $N = 48$). Litter level was excluded from this analysis as a non-comparable trap set. Means were separated by the Tukey honestly significant difference test ($p < 0.05$). Abundance values (Y) were log transformed by the equation $W = \ln (Y + 1)$, prior to the ANOVA to achieve normality assumptions (Basset 1999; Martikainen et al. 2000). Complementary, overlapping graphics (Willott 1999) and cluster analysis, using a complete linkage amalgamation rule and Euclidean distance measurement (Gauch and Whittaker 1981) based on a matrix of individual abundance and RTUs were done, to observe their distribution and relationships among environments. Subsequently, a detrended correspondence analysis (*DCA*) was carried out with RTU abundance and occurrence data (Hill 1979), weighting for rare species. Also, *alpha* (specific richness and Simpson coefficient), *beta* (1—qualitative Jaccard index) and *gamma* diversity (based on the Simpson coefficient) were calculated (Moreno 2001). Additionally, *DCA* was conducted for the main orders separately (excluding singletons) with the environmental groupings defined by cluster analysis to emphasize ecological interrelationships between them.

Results

The influence of forest type, growing season and vertical strata on insect communities

Order, family and RTU richness and abundance varied among habitat types (Table 1). Local singletons

Table 1 Order, family, RTU and singleton richness and abundance of insects captured in *N. pumilio* timber-quality forests and their associated non-timber-quality stands

Site type	Order	Family	RTU	Singleton	Abundance
LF	10	46	153	42	5,741
MHLF	9	43	132	39	4,622
BLR	8	34	102	37	1,399
ÑF	8	27	125	44	3,777
S	9	35	74	33	349
W	7	35	121	44	2,992

RTU = recognizable taxonomic unit; *LF* = *N. pumilio* stand on flat ground; *MHLF* = *N. pumilio* stand on a hillside; *BLR* = edge between *N. pumilio* forest and rangeland; *ÑF* = *N. antarctica* stand; *S* = stream riparian environment in *N. pumilio* forests; *W* = *N. pumilio—N. antarctica* forest wetland

represented 27–45% of the total richness in each site, being highest in *ÑF* and *W*. When abundance was compared (Table 2), Diptera stood out in timber-quality stands (*LF* and *MHLF*) with more than 2,200–3,200 captures; and Lepidoptera dominated in *LF*, *MHLF*, *ÑF* and *W* with more than 1,600–2,300 captures. Overall, the same order dominance pattern was observed in all the forest types (Table 2), except for Lepidoptera in *N. antarctica* forests and wetlands (*DI* of 63% in *ÑF* and 55% in *W*), where it was dominant over Diptera (*DI* of 30% and 38%, respectively). The most important family among the studied orders was Mycetophilidae (Diptera) with a *DI* between a maximum of 40% in timber stands and a minimum of 20% in wetlands. In this family, only two RTUs concentrated more than 5,800 captures (D9 and D10) (Annex 1). Other fly families were less dominant (*DI* < 10%) in all the sites,

except Chironomidae (Diptera) in *S*, where its *DI* reached 13%.

Significant differences were found in average RTU richness and abundance per sampling day, when site types, growing seasons and vertical strata were considered as main factors (Table 3). Among site types, richness and abundance were higher in timber-quality than in associated non-timber-quality stands (Fig. 1). Samples from the flat ground timber-quality forest (*LF*) had greater richness (46 RTUs per sampling day) than *S* and *BLR* (14 and 24, respectively), but did not significantly differ from *MHLF*, *ÑF* and *W* (31–38 RTUs). Abundances were significantly higher in timber-quality forests (*LF* and *MHLF*), as well, with more than 561 individuals per sampling day, while riparian stands (*S*) presented the lowest values (40 individuals per sampling day), and *BLR*, *W* and *ÑF* had intermediate values (168–468 individuals).

At the end of the growing season, richness and abundance per sampling day were higher than at the beginning (46 RTUs and 722 individuals per sampling day compared to 15 RTUs and 51 individuals) (Table 3). Both richness and abundance were significantly highest at the understory level (36 RTUs and 488 individuals per sampling day) and lowest in the overstory canopy (26 RTUs and 285 individuals per sampling day) (Table 3). The leaf litter presented less richness and abundance compared to the other strata (7 RTUs and 14 individuals per sampling day), but this could be the result of only using a single trap type at this level.

Interactions between main factors were not significant for RTU richness and abundance, except for site types and growing season (Table 3). This occurred because several site types presented different responses when they were

Table 2 Total RTU richness and abundance (in parenthesis) shown for insect orders captured in *N. pumilio* timber-quality forests and their associated non-timber-quality stands

		LF	*MHLF*	*BLR*	*ÑF*	*S*	*W*
Orders	*Diptera*	56 (3,260)	47 (2,282)	33 (653)	46 (1,145)	38 (225)	48 (1,136)
	Lepidoptera	27 (1,914)	26 (1,976)	28 (580)	26 (2,394)	12 (74)	27 (1,635)
	Hymenoptera	43 (365)	32 (152)	19 (109)	32 (170)	10 (14)	30 (182)
	Coleoptera	18 (183)	21 (189)	17 (43)	14 (41)	9 (29)	9 (22)
	Homoptera	2 (5)	1 (4)	1 (1)	3 (12)	1 (1)	4 (11)
	Trichoptera	3 (5)	1 (4)	1 (9)	–	1 (1)	2 (5)
	Neuroptera	1 (1)	1 (7)	–	1 (6)	–	–
	Psocoptera	1 (6)	1 (6)	2 (3)	2 (8)	1 (3)	1 (1)
	Hemiptera	–	2 (2)	1 (1)	–	–	–
	Thysanoptera	1 (1)	–	–	1 (1)	–	–
	Ephemeroptera	1 (1)	–	–	–	1 (1)	–
	Plecoptera	–	–	–	–	1 (1)	–
Total		153 (5,741)	132 (4,622)	102 (1,399)	125 (3,777)	74 (349)	121 (2,992)

RTU = recognizable taxonomic unit; *LF* = *N. pumilio* stand on flat ground; *MHLF* = *N. pumilio* stand on a hillside; *BLR* = edge between *N. pumilio* forest and rangeland; *ÑF* = *N. antarctica* stand; *W* = *N. pumilio—N. antarctica* forest wetland; *S* = stream riparian environment in *N. pumilio* forests

Table 3 ANOVA results for average RTU richness and abundance of insects in *N. pumilio* timber-quality forests and their associated non-timber-quality stands are shown for site types, growing season period and vertical strata

Source of variation		RTU richness	Abundance
A: Site type	*F* (*p*)	6.77 (0.0005)	13.05 (0.0000)
	LF	46 c	707 cd
	MHLF	38 bc	561 d
	BLR	24 ab	168 b
	ÑF	31 abc	468 bc
	S	14 a	40 a
	W	33 bc	373 bc
B: Growing season	*F* (*p*)	81.27 (0.0000)	160.35 (0.0000)
	Beginning	15 a	51 a
	End	46 b	722 b
C: Vertical stratum	*F* (*p*)	8.13 (0.0088)	12.44 (0.0017)
	Understory	36 b	488 b
	Canopy	26 a	285 a
F Interaction AB (*p*)		3.91 (0.0098)	4.73 (0.0038)
F Interaction AC (*p*)		1.10 (0.3855)	0.30 (0.9076)
F Interaction BC (*p*)		0.56 (0.4610)	0.33 (0.5691)
F Interaction ABC (*p*)		1.03 (0.4213)	0.25 (0.9365)

RTU = recognizable taxonomic unit; *LF* = *N. pumilio* stand on flat ground; *MHLF* = *N. pumilio* stand on a hillside; *BLR* = edge between *N. pumilio* forest and rangeland; *ÑF* = *N. antarctica* stand; *W* = *N. pumilio*—*N. antarctica* forest wetland; *S* = stream riparian environment in *N. pumilio* forests. Raw data were log transformed using the function W = ln(Y + 1), where Y = abundance and W = transformed abundance. Significance levels are presented in parenthesis, as *p*. Different letters within columns represent significant differences at *P* < 0.05 by Tukey test

compared in the two periods along the growing season. Specifically, *S* presented lower RTU richness and abundance at the end of the growing season than was expected, while *ÑF* and *W* abundances were higher at the end of the growing season than was projected (Fig. 1). This highlighted the fact that differences in site types were not an area effect, because small area sites such as *W* showed greater abundance than larger ones, like *S*.

Insect assemblages in the forest landscape mosaic

Cluster analysis allowed us to assemble the studied site types into three groups: (1) the first was constituted of forest edges (*BLR* and *ÑF*), with higher internal homogeneity; (2) the second was conformed of stands with high water availability (*W* and *S*), connected by a greater Euclidean distance but nearly related to the preceding cluster; and (3) the third set of sites that corresponded to *N. pumilio* timber-quality forests (*LF* and *MHLF*), both of which were very different compared to the others (Fig. 2A). Richness overlap analysis using this grouping showed that 39% of the insect RTUs were widely distributed in all the sites (Fig. 2B), while timber-quality stands had the highest percentage of exclusive RTUs (18% unique to timber-quality forests) with 14% RTUs shared with edge stands and 9% shared with stands with high water availability.

When alpha diversity was analyzed through RTU specific richness, *LF* was the most diverse site with 153 RTUs, while *S* presented the lowest value (74 RTUs). In contrast, the Simpson index, which included community structure parameters (e.g., abundance and evenness) showed *S* and *W* to be the most diverse site types (0.93 for both) and timber-quality stands (*LF* and *MHLF*) were the less diverse (0.89). The same was observed if site type grouping was considered (a greater specific richness for timber-quality forests and greater Simpson index for edges and wet sites). The higher abundance of some RTUs captured in the timber-quality forests (e.g., Dipterans), caused the Simpson index to undervalue the less abundant RTUs, obtaining lower coefficients compared to sites with balanced abundances (*S* and *W*). When beta diversity was analyzed, a higher percentage of shared species was found between *LF* and *ÑF* (0.45), while the greatest dissimilarity was observed between *MHLF* and *S* (0.71). Regarding the site type grouping analysis, timber-quality forests and edge stands were the most similar (0.43) compared to high water availability sites (0.49). The gamma diversity index reached 0.92 in site types or group analysis, with a larger percentage of intra diversity (99.4%) than shared one (0.6%).

In a first *DCA* ordination analysis, the whole sampling data set was analyzed and only axes one and two were used. Plots at the end of the growing season showed the
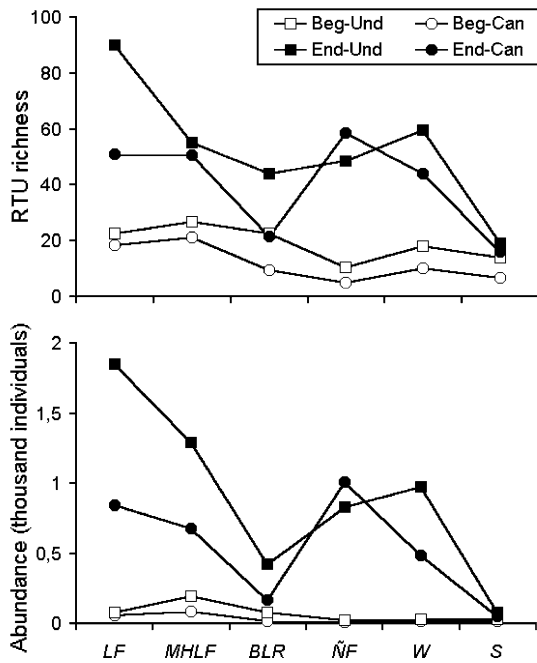
Fig. 1 RTU richness and abundance of insects in two vertical strata and two growing season periods for *N. pumilio* timber-quality forests and their associated non-timber-quality stands. *LF = N. pumilio* stand on flat ground, *MHLF = N. pumilio* stand on a hillside, *BLR* = edge between *N. pumilio* forest and rangeland, *ÑF = N. antarctica* stand, *S* = stream riparian environment in *N. pumilio* forests, *W = N. pumilio—N. antarctica* forest wetland. *Beg-Can* = canopy level at the beginning of the growing season, *End-Can* = canopy level at the end of the growing season, *Beg-Und* = understory level at the beginning of the growing season, *End-Und* = understory level at the end of the growing season
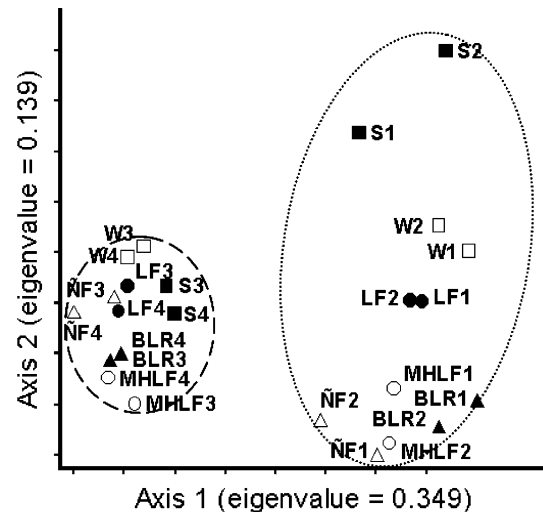

Fig. 3 *DCA* ordination for 24 plots based on insect abundance data. Numbers 1 and 2 correspond to replicate plots in the same site type at the beginning of the growing season, while numbers 3 and 4 correspond to the replicates at end of the growing season. *LF = N. pumilio* stand on flat ground, *MHLF = N. pumilio* stand on a hillside, *BLR* = edge between *N. pumilio* forest and rangeland, *ÑF = N. antarctica* stand, *W = N. pumilio—N. antarctica* forest wetland, *S* = stream riparian environment in *N. pumilio* forests. *Circles* enclose different site type plots according to the period of the sampling season; *dotted lines* are for the beginning, and *dashed line* for the end of the growing season

best cohesion, while plots at the beginning appeared widely distributed (Fig. 3). The observed heterogeneity in the first axis (eigenvalue = 0.349) could be related to the growing season, and the second (eigenvalue = 0.132) to inherent ecological variability, like moisture gradients.

Recognizable taxonomic units of the main four orders in the grouped site types were analyzed in a second *DCA* ordination analysis, and only the first two axes were used as

well (Fig. 4). Coleoptera and Hymenoptera had more RTUs associated with timber-quality forests (Fig. 4B, C) and few related to the other sites types. On the other hand, Diptera and Lepidoptera presented many generalist RTUs (Fig. 4A, D), described as commons or very commons. The timber-quality forest flies were very common RTUs (9/68), mainly from the Mycetophilidae family. In contrast, 12 of 68 RTUs were exclusive to timber-quality forests with nine regional singletons and three rare. Other timber-quality forest exclusive RTUs were 3 of 30 Lepidoptera, just one of which was a regional singleton; 10 of 50 Hymenoptera, with three classified as rare and seven as regional
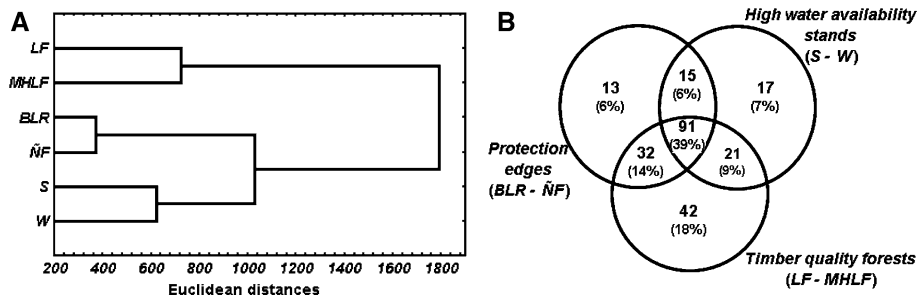

Fig. 2 Cluster analysis (**A**) and species overlapping (**B**) indicating differences between timber-quality and associated non-timber-quality forest site types. *LF = N. pumilio* stand on flat ground, *MHLF = N. pumilio* stand on a hillside, *BLR* = edge between

N. pumilio forest and rangeland, *ÑF = N. antarctica* stand, *S* = stream riparian environment in *N. pumilio* forests, *W = N. pumilio—N. antarctica* forest wetland

Fig. 4 *DCA* ordination for RTUs and environment groups defined by the classification based on insect abundance data of the orders: Diptera (**A**), Coleoptera (**B**), Hymenoptera (**C**) and Lepidoptera (**D**). *LF* = *N. pumilio* stand on flat ground, *MHLF* = *N. pumilio* stand on a hillside, *BLR* = edge between *N. pumilio* forest and rangeland, *ÑF* = *N. antarctica* stand, *W* = *N. pumilio*—*N. antarctica* forest wetland, *S* = stream riparian environment in *N. pumilio* forests. D: Diptera; H: Hymenoptera; C: Coleoptera; L: Lepidoptera. Singletons are not included in the ordination graphs
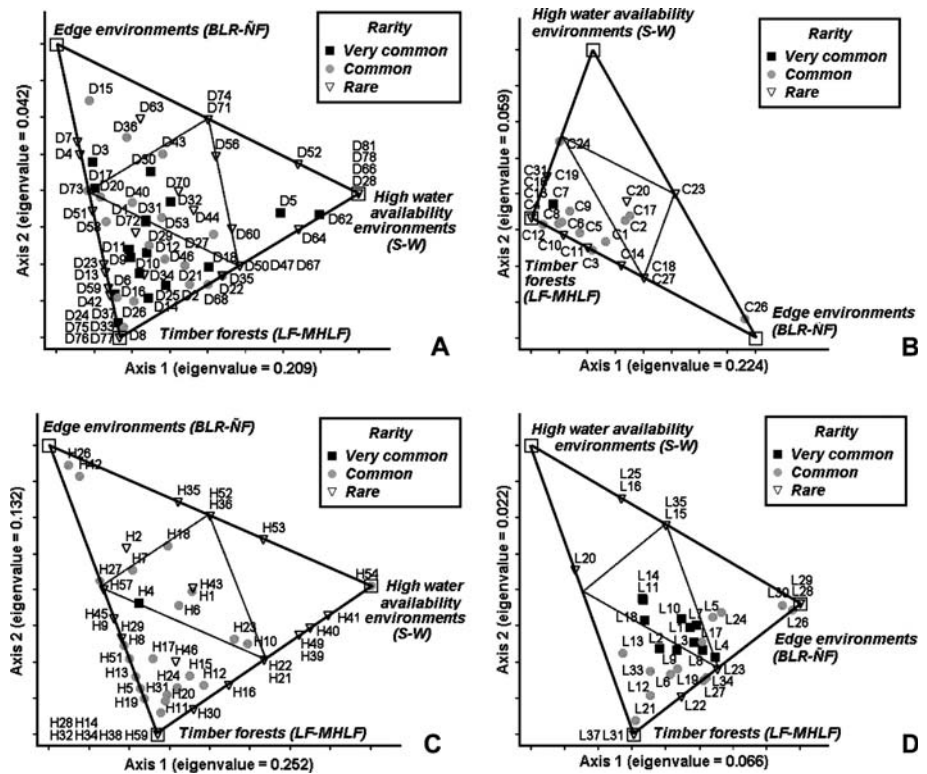
singletons; and 7 of 26 Coleoptera, with three rare and four regional singletons.

Despite the fact that the timber-quality forests hosted the highest proportion of total RTUs, the associated non-timber-quality stands had many exclusive species, mainly from Diptera, Lepidoptera and Hymenoptera. Moths and beetles were scarce in wet sites, and Neuroptera, Tisanopterae and Hemiptera were not found in wetlands at all. In these wet sites, exclusive RTUs were 9 of 59 Diptera (six of them were regional singletons), 3 of 34 Hymenoptera (two regional singletons and one Cynipidae common RTU), only 1 of 27 Lepidoptera (regional singleton) and 1 of 14 Coleoptera (Scolytidae regional singleton). There were also two RTUs for orders of minor importance (a rare Homoptera and a regional singleton Plecoptera). In forest edges, exclusive RTUs were 4 of 22 Coleoptera, 3 of 36 Hymenoptera, 2 of 52 Diptera, 2 of 32 Lepidoptera, and 1 of 9 for orders of minor importance, all of them being regional singletons except moths, which were rare. Complementary, most taxa with specific environmental requirements were collected in timber-quality forests (14 in *LF* and 8 in *MHLF*), while only six were found in *N. antarctica* forests, two in forest wetlands and one in protection edges.

The subantarctic forest insect assemblage

The complete trap system used in this study captured a total of 18,880 individuals, belonging to 231 RTUs from 12 orders and 61 families (Table 4, Annex 1 and 2). Dominant orders had both the greatest richness and abundance, and included Diptera, Lepidoptera, Hymenoptera and Coleoptera (*DI* of 46%, 45%, 5% and 3%, respectively). The other orders were relatively scarce (*DI* between 0.01–0.20%).

Table 4 Superfamily, family and RTU richness, individual abundance and dominance index are shown for insect orders captured in *N. pumilio* timber-quality forests and their associated non-timber-quality stands

Order	Super-family	Family	RTU	Abundance	Dominance index
Diptera	12	22	83	8,701	46.1
Lepidoptera	?	?	37	8,573	45.4
Hymenoptera	6	9	60	992	5.2
Coleoptera	8	18	33	507	2.7
Homoptera	4	4	5	34	0.2
Trichoptera	2	2	3	24	0.1
Neuroptera	1	1	2	14	0.1
Psocoptera	?	?	2	27	0.1
Hemiptera	2	2	2	3	0.02
Thysanoptera	1	2	2	2	0.01
Ephemeroptera	–	1	1	2	0.01
Plecoptera	1	1	1	1	0.01
Total	37	61	231	18,880	100

RTU = recognizable taxonomic unit; ? = undetermined to family or superfamily level

The most diverse Diptera families were Chironomidae (11 RTUs), Tipulidae and Mycetophilidae (10 RTUs each). All Lepidoptera captures belonged to the Heterocera suborder, including macro and micro-lepidopterans. The most important Hymenoptera families were Ichneumonidae (71% captures and 26 RTUs), followed by Cynipidae (19% captures and 10 RTUs) and Braconidae (5% captures and 13 RTUs). Coleoptera had Scarabaeidae and Cryptophagidae as the most abundant families (41% and 15% of the order captures, respectively). Meanwhile, Staphylinidae was the most diverse beetle family (five RTUs).

Many of the Diptera RTUs were rare (31 of 83 RTUs), while the other categories presented similar proportions (17 of 83 very common RTUs, 18 common and 17 singletons) (Annex 3). Lepidoptera regional singletons were few (2 of 37 RTUs), and the other categories were equivalent (11 of 37 very common, 13 common and 11 rares). On the other hand, Hymenoptera had many common taxa (22 of 60), rare RTUs (25), and some regional singletons (12) with only one very common RTU (Ichneumonidae). Coleoptera rarity was similar to Hymenoptera, with numerous common, rare and regional singleton RTUs (11, 12 and 9 of 33, respectively), and only one very common RTU (Scarabeidae). Orders of minor importance that had few common RTUs included one Trichoptera and one Psocoptera.

Discussion

The value of the timber-quality forests for insect conservation on Tierra del Fuego Island

Insect diversity found in timber-quality forests was significantly higher than in the associated non-timber-quality stands. Their unique ecological conditions related with a greater overstory and understory habitat heterogeneity (Lencinas 2005) facilitate the survival of exclusive taxa and RTUs with specific environmental requirements, which appear rarely in most sites but could be very abundant in others. This heterogeneity determines the existence of a low proportion of generalist taxa, mainly Lepidoptera, Hymenoptera, Diptera and Psocoptera. Habitat heterogeneity increases the variety of available niches for colonization, and consequently the richness that this could support (Ozanne et al. 2000). For example, the soil depressions left by the roots of wind-thrown trees and hollowed trunks can fill with rain water in timber forests, that makes them appropriated niches for Chironomidae (Diptera) aquatic larvae development (Pérez et al. 1997) even in upland forests.

On the other hand, insectivorous bird density has been found to be greatest in open clearings, such as W and S

(Lencinas et al. 2005), which could diminish insect abundance, e.g. Lepidopteran. In edge sites, the lower diversity was contrary to that described by Kotze and Samways (1999) for carabids and amphipods in Afromontane forests, probably due to the scarce herbaceous diversity layer and the extreme environmental conditions (strong winds and lower temperatures) observed in *Nothofagus* forests. Insect diversity in the non-timber-quality stands was only greater than in the timber-quality forests for those orders that need specific ecological conditions only available in these stands (e.g. water courses for Ephemeroptera and Plecoptera larvae available only in S).

Designing forest management plans that include insect conservation

Insects are vulnerable to habitat loss, as are any organisms. *Nothofagus pumilio* forests have an endemic entomofauna, which includes unique, rare and relict species (Lanfranco 1977; McQuillan 1993) of great importance to define biogeographic regions (Niemelä 1990; Roig-Juñent et al. 2002) as to they are the world's southernmost species, genera, families and even orders.

Several cutting cycles have been historically applied in *Nothofagus* forests to make natural regeneration possible, or to facilitate the process by opening the canopy, varying from light selective cuts to clear-cuts (Gea et al. 2004). The most widely used method has been the shelterwood cut (Martínez Pastur et al. 2000; Rosenfeld et al. 2006), which opens the overstory canopy and increases light availability up to threefold, effective rainfall at the understory level (Caldentey et al. 2005a), global radiation, temperature and wind speed, in the process causing greater evapotranspiration (Caldentey et al. 2005b). Shelterwood cuts cause a large impact on insect diversity with one species lost every 11 years during the first silviculture cycle, and allow the introduction of species from other site types that quickly colonize the impacted stands (Spagarino et al. 2001). Also, shelterwood cuts not only affect insect communities, but produce changes in forest use, diversity and density of many other species (plants, birds and mammals), and modify their inter-specific relationships (Martínez Pastur et al. 1999, 2002; Pulido et al. 2000; Deferrari et al. 2001).

Biodiversity conservation in managed landscapes could be improved by maintaining the associated non-timber-quality stands (Lencinas et al. 2005), where species could survive until the forest structure of the harvested timber-quality forest will be recovered. However, this alternative does not offer a solution for insect conservation at the landscape level, as we have found that many insect taxa only inhabited timber-quality stands.

Several alternative silvicultural methods (Franklin et al. 1997) have been proposed for the *Nothofagus pumilio*

forests, which conserve some of the original heterogeneity of the old-growth forest. Bava and López Bernal (2005) proposed to selectively cut groups affecting a small percentage of the forest area, while another method proposes to leave several degrees and retention types of the original old-growth forests (Martínez Pastur and Lencinas 2005; Martínez Pastur et al. 2005; Vergara and Schlatter 2006). This last method has been shown to improve the conservation of the original timber-quality forest's biodiversity (Martínez Pastur et al. 2005; Vergara and Schlatter 2006), which is especially relevant for insect conservation. However, the size, shape and distribution of the retention in the timber forest, as well as the distribution patterns of the different types of unproductive associated stands throughout the forest landscape, must be evaluated to achieve better long-term conservation. For this purpose, the Before–After–Control–Impact (BACI) approach is highly recommended to control for environmental variation between sites and the year-to-year fluctuation in several environmental conditions (Niemelä 2001).

Insect diversity in subantarctic Nothofagus forests

Temperate forest entomofauna from the northern and southern hemispheres is unequally known. In boreal forests, the knowledge acquired to date has allowed a conservation status to be designated for many insect species affected by human impacts (Martikainen et al. 2000; Niemelä 2001). In sharp contrast, subantarctic South American temperate forests contain a largely unknown insect assemblage, which has yet to be fully described (Lanfranco 1977; Stary 1994). Thus, there is not enough information on their capture locations, as well as the related vegetation community (Giganti and Dapoto 1990; Giganti et al. 1994; Shapiro 1997), autecology, habitat requirements or economic importance.

We can say that entomofauna richness of *Nothofagus* forests follows the pattern of generally poorer faunal diversity in southern Patagonia (Guzmán et al. 1985–1986) compared to northern regions of similar latitudes (Martikainen et al. 2000). This low diversity is probably related to the short growing season (Roig et al. 2002) and the lower average summer temperatures in the subantarctic forests (Ferreyra et al. 1998). For example, the scarce Coleopteran diversity described to date for Fuegian forests (33 RTUs in this study; 9 species by Berg 1899; and 16 by Bruch 1925) is relatively low compared to 192 beetle taxa in hardwoods forests of the Great Lakes Region between the United States and Canada (Werner and Raffa 2000) or 553 in forests of southern Finland (Martikainen et al. 2000). Low diversity could be the explanation for the few singletons observed in this work too. Singletons could represent half the richness in other insect inventories

(Lewis and Whitfield 1999; Novotný and Basset 2000). However, it is possible that some insect species of the Fuegian forests were not studied or captured yet, thus currently an underestimation of their real diversity likely exists.

In this work, the inclusion of different kinds of forests, the use of wide spectrum trap systems and the sampling design throughout the growing season improved the diversity estimates compared to previous studies in *Nothofagus* forests. Here, 231 RTUs were defined, while 9 to 55 species were registered in recently deglaciated areas of the Darwin Mountains in the Chilean portion of Tierra del Fuego Island (Pérez et al. 1997) and nearly 200 RTUs in the Magallanes Region of Chile (Lanfranco 1991). In timber stands, we found 132–153 RTUs, which was comparable to those found in other forests of the central zone on Tierra del Fuego with the same trap system (104 RTUs described by Spagarino et al. 2001).

The seasonal variability of *Nothofagus* forest insect richness showed a low degree of insect community maturity in the beginning of the growing season and its low community stability with large fluctuations over the study period (Lanfranco 1991). The higher abundance and richness at the end of the growing season can be related to the more benign climatic conditions and the greater understory plant availability in summer than spring (Lencinas 2005). On the other hand, highest richness at the understory level observed in this work differs from Whitaker et al. (2000), who found more richness at the canopy level in northern USA forests. This hemispheric difference could be due to the higher wind exposure confronted by the austral forest canopy and the mono-specific overstory composition, which offer less food and shelter than multi-specific and multi-layer forests. In contrast, much of the varied plant species composition at the understory level sustained a higher insect diversity, as well as associated diversity of arachnids, birds and small mammals.

Alpha diversity indexes are widely used in insect studies (e.g., Arellano and Halffter 2003; Willott 1999), but comparisons are difficult due to the results differ according to the community structure analyzed, as was presented here. In this study, taxa richness was more useful than the Simpson index, but their use as a measure of biological conservation value may be misleading, because disturbances may favor widespread and abundant generalists leading to increased species richness. For this reason, "rarity values" or "rarity scores" of sites (or species assemblages) can be used in combination with species richness to provide a measure of the conservation value of a site (Niemelä 2001).

In contrast, beta diversity indexes have been poorly employed on insect studies (Willott 1999; Arellano and Halffter 2003; MacNally et al. 2004). The low values of

beta diversity found in this study were due to the scarce presence of generalist species compared to the existing RTUs with specific environmental requirements. Also, beta diversity can be reduced due to species introductions, which can compete with native species for resources and modify the natural system and biotic relationships. Finally, gamma index composition enhances the significance of the intrinsic diversity in each forest habitat compared to the shared one, which was described by Arellano and Halffter (2003) for Coleopterans in Veracruz (Mexico).

The observed order dominance was similar to other *Nothofagus* forests (Lanfranco 1991; Spagarino et al. 2001), as well as to other Patagonian forest types (Coscarón and Wygodzinsky 1962; Pérez et al. 1997), independent of the trap system employed. Mycetophilidae and Tipulidae (Diptera), whose larvae feed mainly on mushrooms, presented the highest dominance, which could be related to the varied decomposition state of many standing trees inside the primary forests (Lanfranco 1977; Pérez et al. 1997) and the large presence of woody debris over the forest floor (Lencinas 2005). Also, the abundance of saprophagous Scarabeidae and mycetophagous Cryptophagidae (Coleoptera) are related to dead wood too (Martikainen et al. 2000).

Hymenoptera is well represented in *Nothofagus* forests. Ichneumonidae, the most important family, and Braconidae presence can be associated with its host larvae (Lepidopterans, Coleopterans, Homopterans and Dipterans), but it is quite difficult to relate them to any particular plant community (Lanfranco 1974). RTU Cynipidae richness was probably overestimated (10 RTUs in this study), due to the high heterogeneity of their morphological characters (agamous and sexual reproduction) (Richards and Davies 1984). However, these species generally attack only one plant species, which is *Espinosa nothofagi* for *Nothofagus pumilio* forests (Lanfranco 1991).

Heterocera predominates in the Lepidoptera order, due to the cold shadow environments and the scarce nutritious food (plants with flowers), which is not adequate for day time butterflies (Shapiro 1997). Giganti et al. (1994) designate the Geometridae, Cossidae and Saturniidae as the most characteristic families for *Nothofagus* forests. Finally, the orders of minor importance are cited as mono-specific for *N. pumilio* forests by Lanfranco (1991) (Homoptera, Psocoptera and Hemiptera), although in this study two to five RTUs where found for each.

It should be noted also that the diversity of insects found in water-associated forest sites, such as forested wetlands and stream riparian zones, could be higher than that which we report here. In these ecosystems many of the associated taxa develop part or all of their life cycle in the aquatic habitat and emerge for only short periods as adults to reproduce. To date, the in-stream insect diversity is known to include at least 22 taxa in the Alberto de Agostini National Park, Chilean Tierra del Fuego (Moorman et al. 2006); 27 in the Cape Horn Biosphere Reserve, Chile (Anderson and Rosemond, in press); and an archipelago-wide total of 42 (Anderson et al. 2007). However, these insects' life histories, their emergence patterns and their associated terrestrial habitat needs still remain largely unknown. In any event, upland, timber-quality forests are still apparently the major reservoir of insect diversity in the subantarctic landscape, but a greater understanding of terrestrial/aquatic linkages in wetland and riparian ecosystems could increase the conservation value of these habitat types.

Conclusions

Here, we have shown that timber-quality forest stands are extremely important for the conservation of insect communities in subantarctic forest landscapes in the Tierra del Fuego-Cape Horn Archipelago. *Nothofagus pumilio* timber-quality stands supported a relatively high number of insect species, compared to other habitat types found in these, the world's southernmost forests. In addition, many of the taxa found in timber-quality forests are only found there and do not inhabit the associated non-timber-quality stands. Consequently, the importance of the associated non-timber-quality stands for insect conservation is limited as exclusive species only represent 19%, while those shared with the timber-quality forests are more than half (62%). The fact that a large portion of the non-exploitable forest's insect community is shared with the commercial forests means that they can be a source of colonists to aid the recuperation of species loss when the forest structure of timber-quality stands is impacted during forest management. It should be noted, however, that as 42% of the timber-quality forest's insect community were only found there, in terms of landscape level conservation, associated non-timber-quality stands are not sufficient to recuperate pre-harvest diversity. Therefore, protection of associated non-timber-quality forests in a managed landscape will not be sufficient to maintain insect communities in the subantarctic archipelago.

To adequately maintain this diverse landscape mosaic, more research on the key insect groups and taxa of timber-quality forests is needed to develop adequate forest management strategies that increase species protection and at the same time minimize the impacts to these communities during the forest management cycle. Alternative silviculture techniques that improve the conservation of insect groups in timber-quality forests must be developed (e.g., regeneration cuttings with aggregated and dispersed retention) in order to maintain and/or recuperate faster from the changes in the original insect diversity.

Appendix

Annex 1 A complete list of the taxa found during the study (part 1)

Order	Suborder	Superfamily	Family	RTUs
Diptera	Nematocera	Tipuloidea	Tipulidae	*10 (D2, D5, D6, D47, D48, D65, D67, D74, D80, D84)*
		Anisopodoidea	Anisopodidae	*1 (D24)*
		Bibionoidea	Bibionidae	*1 (D39)*
		Culicoidea	Ceratopogonidae	*1 (D16)*
			Chironomidae	*13 (D12, D18, D22, D26, D29, D31, D32, D50, D53, D59, D60, D66, D75)*
			Simuliidae	*3 (D13, D15, D19)*
		Mycetophiloidea	Cecidomyidae	*3 (D25, D27, D35)*
			Mycetophilidae	*10 (D1, D9, D10, D17, D34, D43, D56, D68, D73, D78)*
			Sciaridae	*2 (D14, D76)*
	Brachycera	Empidoidea	Dolichopodidae	*1 (D77)*
			Empididae	*3 (D23, D33, D42)*
		Tabanoidea	Rhagionidae	*3 (D7, D58, D64)*
			Tabanidae	*1 (D20)*
	Cyclorrhapha	Agromyzoidea	Otitidae	*1 (D37)*
			Chyromyidae	*2 (D3, D11)*
			Heleomyzidae	*2 (D4, D71)*
		Drosophiliodea	Drosophilidae	*2 (D46, D52)*
			Ephydridae	*1 (D28)*
		Lonchopteroidea	Lonchopteridae	*1 (D62)*
		Muscoidea	Muscidae	*7 (D21, D44, D51, D8, D40, D63, D72)*
			Fannidae	*1 (D70)*
		Phoroidea	Phoridae	*2 (D30, D36)*
	Not determined			*12 (D38, D41, D45, D49, D54, D55, D61, D69, D79, D81, D82, D83)*
Hymenoptera	Symphyta	Tenthredinoidea	Tenthredinidae	*1 (H44)*
	Apocrita	Chalcidoidea	Eulophidae	*3 (H10, H35, H58)*
			Eurytomidae	*2 (H14, H21)*
			Pteromalidae	*2 (H31, H41)*
		Cynipoidea	Cynipidae	*10 (H11, H13, H15, H17, H22, H24, H28, H32, H54, H55)*
		Ichneumonoidea	Braconidae	*13 (H9, H19, H29, H33, H34, H38, H40, H43, H47, H48, H49, H52, H53)*
			Ichneumonidae	*26 (H1, H2, H3, H4, H5, H6, H7, H8, H12, H16, H18, H20, H23, H26, H27, H36, H37, H39, H42, H45, H46, H50, H51, H57, H59, H60)*
		Scelionoidea	Scelionidae	*1 (H30)*
		Scolioidea	Tiphiidae	*2 (H25, H56)*

D: Diptera; *H*: Hymenoptera

Annex 2 A complete list of the taxa found during the study (part 2)

Order	Suborder	Superfamily	Family	RTUs
Coleoptera	Adephaga	Caraboidea	Carabidae	*4 (C12, C15, C18, C24)*
	Polyphaga	Cantharoidea	Ptinidae	*1 (C19)*
		Chrysomeloidea	Cerambicidae	*1 (C26)*
			Chrysomelidae	*2 (C3, C30)*
		Cucujoidea	Ciidae	*1 (C25)*
			Cryptophagidae	*1 (C5)*
			Cucujidae	*1 (C1)*
			Erotylidae	*1 (C4)*
			Mycetophagidae	*1 (C21)*
			Tenebrionidae	*1 (C31)*
		Curculionoidea	Anthribidae	*1 (C33)*
			Curculionidae	*4 (C22, C27, C28, C29)*
			Brenthidae	*1 (C20)*
			Scolytidae	*4 (C14, C17, C32, C8)*
		Histeroidea	Histeridae	*1 (C6)*
		Scarabaeoidea	Scarabaeidae	*2 (C2, C7)*
		Staphylionoidea	Ptiliidae	*1 (C10)*
			Staphylinidae	*5 (C9, C11, C13, C16, C23)*
Lepidoptera	Not determined			*37 (L1 to L37)*
Ephemeroptera	–	Leptophlebioidea	Leptophlebiidae	*1 (E1)*
Plecoptera	Setipalpia	Perloidea	Chloroperlidae	*1 (Ple1)*
Psocoptera	Trocomorpha	?	?	*1 (P1)*
	Psocomorpha	?	?	*1 (P3)*
Thysanoptera	Tubulifera	–	Phlaeothripidae	*1 (Thy3)*
	Terebrantia	Thripoidea	Thripidae	*1 (Thy4)*
Hemiptera	Gymnocerata	Cimicoidea	Nabidae	*1 (He2)*
		Lygaeoidea	Lygaeidae	*1 (He3)*
Homoptera	Sternorrhyncha	Psylloidea	Psyllidae	*2 (Ho2, Ho4)*
		Coccoidea	Coccidae	*1 (Ho3)*
		Aphidoidea	Aphididae	*1 (Ho5)*
	Auchenorrhyncha	Cicadelloidea	Cicadellidae	*1 (Ho1)*
Neuroptera	Planipennia	Hemerobioidea	Hemerobiidae	*2 (N1, N2)*
Trichoptera	Integripalpia	Limnephiloidea	Limnephilidae	*2 (T1, T2)*
		Rhyacophiloidea	Hydroptilidae	*1 (T3)*

C: Coleoptera; *L*: Lepidoptera; *E*: Ephemeroptera; *Ple*: Plecoptera; *P*: Psocoptera; *Thy*: Thysanoptera; *He*: Hemiptera; *Ho*: Homoptera; *N*: Neuroptera; *T*: Trichoptera; *?*: undetermined to superfamily or family level

Annex 3 Recognizable Taxanomic Unit (RTU) rarity

Order	Very commons	Commons	Rares	Singletons
Diptera	*D1, D3, D5, D6, D9, D10, D11, D12, D14, D17, D18, D25, D30, D31, D32, D37, D62*	*D2, D8, D15, D16, D36, D20, D21, D26, D27, D29, D35, D40, D43, D46, D53, D58, D68, D73*	*D4, D7, D13, D22, D23, D24, D28, D33, D34, D42, D44, D47, D50, D51, D52, D56, D59, D60, D63, D64, D66, D67, D70, D71, D72, D74, D75, D76, D77, D78, D81*	*D19, D38, D39, D41, D45, D48, D49, D54, D55, D61, D65, D69, D79, D80, D82, D83, D84*
Lepidoptera	*L1, L2, L3, L4, L7, L8, L9, L10, L11, L14, L18*	*L5, L6, L12, L13, L17, L19, L21, L24, L26, L27, L30, L33, L34*	*L15, L16, L20, L22, L23, L25, L28, L29, L31, L35, L37*	*L32, L36*
Hymenoptera	*H4*	*H1, H5, H6, H7, H8, H10, H11, H12, H13, H15, H17, H18, H19, H20, H23, H24, H26, H27, H31, H42, H51, H54*	*H2, H9, H14, H16, H21, H22, H28, H29, H30, H32, H34, H35, H36, H38, H39, H40, H41, H43, H45, H46, H49, H53, H52, H57, H59*	*H3, H25, H33, H37, H44, H47, H48, H50, H55, H56, H58, H60*
Coleoptera	*C7*	*C1, C2, C3, C5, C6, C8, C9, C12, C17, C26, C24*	*C4, C10, C11, C13, C14, C16, C18, C19, C20, C23, C27, C31*	*C15, C21, C22, C25, C28, C29, C30, C32, C33*
Homoptera		*Ho2*	*Ho1, Ho3, Ho4, Ho5*	
Psocoptera		*P3*	*P1*	
Trichoptera		*T3*	*T1*	*T2*
Neuroptera		*N1*		*N2*
Hemiptera			*He2*	*He3*
Thysanoptera				*Th3, Th4*
Ephemeroptera			*E1*	
Plecoptera				*Ple1*

D: Diptera; *H*: Hymenoptera; *C*: Coleoptera; *L*: Lepidoptera; *E*: Ephemeroptera; *Ple*: Plecoptera; *P*: Psocoptera; *Thy*: Thysanoptera; *He*: Hemiptera; *Ho*: Homoptera; *N*: Neuroptera; *T*: Trichoptera

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