Entomology in Ecuador: Recent developments and future challenges

Olivier Dangles [(1),(2)], Álvaro Barragán [(1)], Rafael E. Cárdenas [(1)], Giovanni Onore [(3)] & Clifford Keil [(1)]

[(1)] Museo de Zoología QCAZ, Sección Invertebrados, Pontificia Universidad Católica del Ecuador, Apartado 17-01-2184, Quito, Ecuador

[(2)] IRD-LEGS, University Paris-Sud 11, F-91190 Gif-sur-Yvette, France

[(3)] Fundación Otonga, Apartado 17-03-1514A, Quito, Ecuador

Abstract. We review and analyze the recent development and future challenges facing entomology as a science in Ecuador, a country with limited financial and human resources and numerous environmental problems. Taxonomic studies of the Ecuadorian insect fauna have been well developed for only a few groups (e.g. Papilionoidea, Carabidae) and remains in its infancy for most insect orders. This is due to the huge diversity of species living in a great diversity of habitats and the difficulty to identify most species. There is a lack of published basic biological information and to a high rate of endemism of many groups, especially in the Andes. The development of ecological entomology as a formal discipline in Ecuador is a very recent phenomenon, and has been mostly limited to descriptive studies of the environmental factors that govern insect diversity and abundance. We outline a set of research challenges regarding the impact of global environmental changes on insect communities and habitats they live in and propose potential strategies for the development of entomology in Ecuador. Both basic and applied research will be important in this context as well as international collaboration to strengthen the role of entomological science in decision making processes in the country.

Résumé. L'entomologie en Equateur : développements récents et futurs défis. Cet article est une révision et une analyse des récentes avancées et des futurs challenges de l'entomologie en tant que science en Equateur, pays dont les ressources financières et humaines sont limitées et qui fait face à de nombreux problèmes environnementaux. La taxonomie de l'entomofaune d'Equateur a été étudiée en détail pour seulement quelques groupes (e.g. Papilionoidea, Carabidae) et reste fragmentaire pour la plupart des ordres d'insectes. Ceci est lié à l'existence d'une très grande diversité d'espèces vivant dans une grande diversité d'habitats et de la difficulté d'identifier la plupart de celles-ci. A cela s'ajoutent un manque réel de données publiées sur la biologie de la plupart des espèces ainsi qu'un fort taux d'endémisme de plusieurs groupes, notamment dans la région andine. Le développement de l'écologie entomologique en tant que discipline en Equateur est un phénomène très récent principalement restreint à des études descriptives sur les facteurs environnementaux qui influencent la diversité et l'abondance des insectes. Nous présentons des thématiques de recherches d'enjeu pour les futures années, notamment en relation avec l'étude de l'impact des changements globaux sur les communautés d'insectes et leurs habitats et nous proposons des stratégies pratiques pour le développement de l'entomologie en Equateur. Dans ce contexte, le développement combiné de la recherche fondamentale et appliquée, si possible dans le cadre de collaborations internationales, permettra de renforcer le rôle de l'entomologie dans les processus de décision à l'échelle du pays.

Keywords: Insect taxonomy, Ecology and evolution, Pests, Monitoring, Global changes.

The Neotropical region has long been recognized as supporting one of the highest levels of biological diversity in the world. Insects are particularly abundant and species rich in many Neotropical ecosystems, yet the extent of this diversity, the factors that govern its distribution and the degree of degradation as a result of anthropogenic changes are still incompletely known. The wide diversity of habitats that Ecuador possesses in a small area makes it an ideal location for biodiversity, ecological and evolutionary research. Although the diversity of many groups (e.g. plants, birds and frogs) has been the focus of numerous publications, data on the entomological fauna in Ecuador are still very incomplete. In this paper, we aim to review and analyze recent developments and future challenges facing entomology as a science in Ecuador, a country with limited financial and human resources and numerous environmental problems. It is not our goal to present a comprehensive review of every paper in entomology published on the Ecuadorian insect fauna, but rather to cite studies, especially those published by, or in collaboration with, Ecuadorian entomologists, that we have found especially important and revealing to illustrate the development of entomology as a science in Ecuador.

E-mail: dangles@legs.cnrs-gif.fr

Accepté le 2 avril 2009

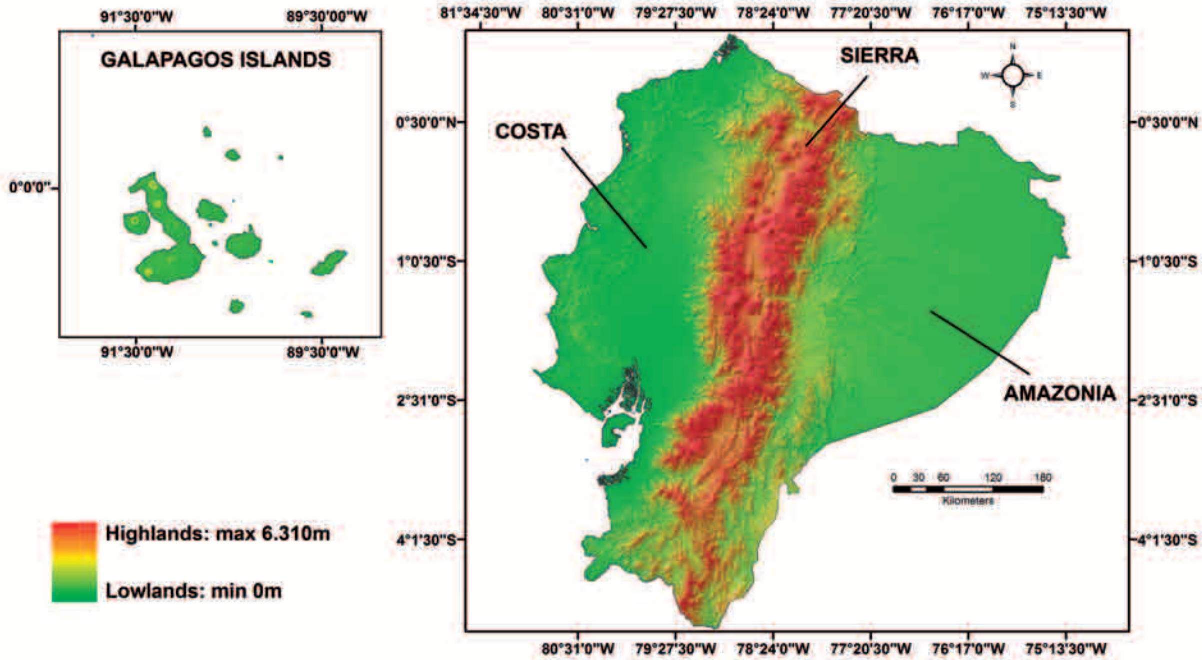


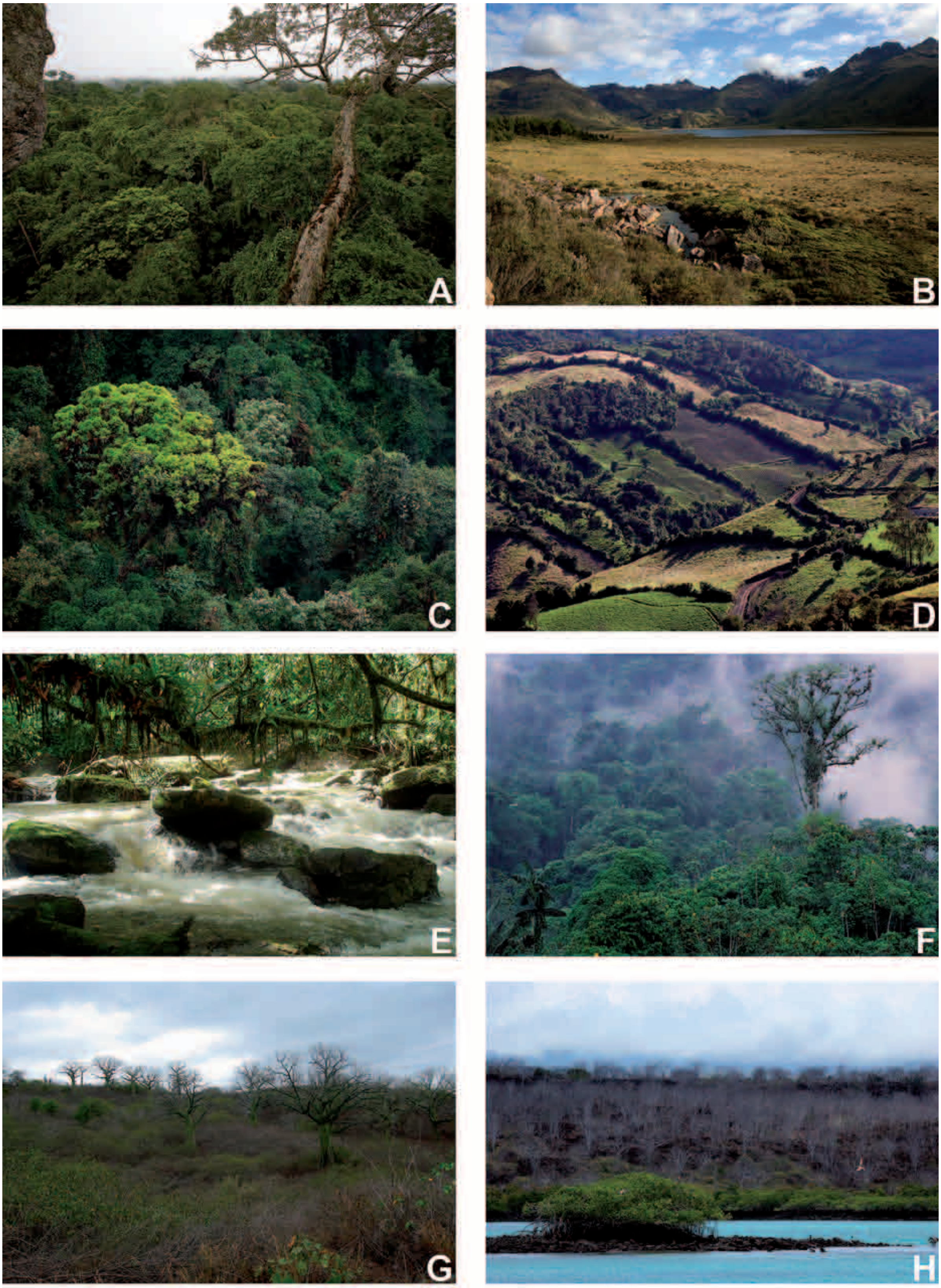
Figure 1
Digital elevation map of Ecuador, including Galápagos Islands. Color bar indicates elevation range.

Ecuador's biogeographic zones

The tropical Andes span more than 1.5 million km^2 from western Venezuela to northern Chile and Argentina, and include large portions of Colombia, Ecuador, Peru, and Bolivia. Ecuador is located in the Northern part of the region, bordered by Peru in the south and southeast, Colombia in the north and northeast and the Pacific Ocean in the west. With an area of only 283.560 km^2, Ecuador is one of the smallest countries of South America. The great highs and lows of the Andes mountain range (fig. 1), with its snowcapped peaks, steep slopes, deep canyons, and isolated valleys, have led to the evolution of an amazing diversity of ecosystems, habitats and thus, species diversification (Hughes & Eastwood 2006; Chaves *et al.* 2007; Ribas *et al.* 2007). Recent studies demonstrate that Andes uplift was separated by relatively long periods of stability (tens of millions of years), and by rapid changes of 1.5 Km or more in relatively short periods of time (1 to 4 million years) (Garzione *et al.* 2008). This allowed the creation of new climatic and environmental niches in relatively short periods of times, and the adaptation of organisms to those habitats for long periods of time. The large variety and range of climatic regimes found in Ecuador have a major effect on the range of vegetation types that define biogeographic zones (see Cárdenas *et al.*, this issue). Ecuador's territory is usually divided into four main natural regions: the Amazonian lowlands, the Andes, the Pacific coastal lowlands and the Galápagos Islands (fig. 1). We provide a short description of each region, which we think will guide the reader not only in this article, but also throughout the special issue. More details on the different biogeographic zones can be found in Ron *et al.* (in press).

Accounting for almost 40% of the total area of Ecuador, the Amazonian region gradually descends eastwards from the foothills of the Andes to altitudes of 200–400 m. The climate is tropical, humid and aseasonal. Monthly mean precipitation is approximately 2820 mm/ year with no month receiving less than 100 mm of rain (Valencia *et al.* 2004). Temperatures range from 22 °C (minima) to 32 °C (maxima). The absence of a prolonged dry season, together with warm temperatures throughout the year and a varied topography, make the region a hotspot of biodiversity (Myers *et al.* 2000). The only biogeographic region of this zone is the evergreen lowland wet forest with a canopy mostly 15–30 m tall and emergent trees reaching 50 m (fig. 2A).

The Ecuadorian Andes occupy the central third of Ecuador and are divided into two main cordilleras,


A
B
C
D
E
F
G
H

western and eastern. Transverse mountain bridges interconnect these two cordilleras forming ten inter-Andean basins with at least 30 peaks of volcanic origin and 25 mountains above 4,500 m (Ron *et al.* in press). The cordillera exhibit precipitous elevation gradients with a complex topography which creates a landscape with extreme climatic differences. Annual rainfall varies between less than 500 mm in the dry inter-Andean basins to above 6000 mm on the Eastern slope. Temperature varies as a function of elevation with small seasonal changes. Major biogeographic regions from East to West include Eastern foothill forest, Eastern montane forest (cloud forest), Páramo, Andean shrub, Western montane forest and Western foothill forest (figs. 2B, C, E).

On the Western slope of the Andes, the Pacific coast contains lowlands, river valleys, and a coastal cordillera with maximum elevations of 800–900 m. Natural ecosystems are dry scrub, deciduous forest, Chocó tropical forest, mangroves and Western montane forests at higher altitudes (mainly in Guayas and Esmeraldas provinces). Characterized as one of the wettest non-seasonal climates on Earth, the Chocó region is another of the top ten hotspots of biodiversity (Myers *et al.* 2000), (fig. 2F). Between the humid Chocoan forest and the dry Peruvian deserts, the dry coastal tropical forest is characterized by a North to South humidity gradient giving it a tremendous complexity of local climates and a great diversity of ecosystems (fig. 2G).

The Galápagos Archipelago comprises 12 large and numerous smaller islands and exposed rocks that have a total area of about 8,000 km². All islands are oceanic and have never been connected to the continent by any sort of land bridge (Constant 2006). Located in the Pacific Ocean approximately 1000 km west of the continent, the Galápagos have a remarkably seasonal climate, largely influenced by shifts in cool water masses originating from the South of Peru and warm water masses from the North (Kricher 2006). Large islands have an altitudinal gradient of vegetation types from arid and transitional forests in the lower parts to moist forest and fern-sedge zones in the higher elevations (Grant 1999, fig. 2H). The volcanic origin of these islands, many of which still have highly active volcanoes, has resulted in celebrated levels of species diversification and endemism (Kricher 2006).

Figure 2
Photographs of some insect rich-ecosystems of Ecuador A. Canopy view of the Amazonian tropical forest (Yasuni National Park, 300 m a.s.l.), B. High altitude grasslands of páramo (Sangay National Park, 3600 m a.s.l.), C. Western montane forest (Yanacocha Reserve, 3200 m a.s.l.), D. Agricultural landscape (Carchi Province, 2800 m a.s.l.), E. Tropical rain forest (Misahuallí, 300 m a.s.l), F. Chocó evergreen forest (Canande Reserve, 1200 m a.s.l.), G. Coastal dry forest (300 m. a.s.l.), H. Coastal mangroves and arid forest (Galápagos National Park). Photo credits: A-D, H: O. Dangles; E: M. Guerra-V.; F: R. E. Cárdenas; G: G. Ramón.

Recent advances in the entomological knowledge in Ecuador

Taxonomy and distribution

Since the creation of the Invertebrate Section of the Museum of Zoology QCAZ of the Pontifical Catholic University of Ecuador (PUCE) in 1981 (see Barragán *et al.* this issue), investigations on entomology have focused mainly on the taxonomy and the biology of specific groups of insects. As in many entomological museums, two taxonomic groups have been the focuses of interest by both local and foreign entomological taxonomists: Lepidoptera and Coleoptera. Note that few other extensive entomological studies have been performed in specific regions of Ecuador such as the work by Peck (2001) on orders of insects of the Galápagos Islands

A database of Ecuadorian butterfly diversity and distribution has been developed by K. Willmott from the Florida Museum of Natural History and J. Hall from the National Museum of Natural History (online access: *http://www. butterfliesofecuador.com*). In addition to the information found on the "butterfly of Ecuador website", four monographs have been published on Lepidoptera genera (Piñas & Manzano 1997), Arctiidae (Piñas & Manzano 2003a), Saturnidae (Piñas & Manzano 2003b), Papilionidae (Bolino & Onore 2001), and Sphingidae (Guevara *et al.* 2002). Willmott & Hall (2008) estimate that Ecuador contains approximately 2700 species of Papilionoidea, about 50–55% of all Neotropical butterfly species and 25% of the world's species, making it one of the world's three most diverse countries along with Colombia and Peru. Exhaustive butterfly inventories in specific Ecuadorian regions over a single year, such as in the Amazonian forest with about 20,000 individuals collected (Checa 2006), and in the Chocó where about 10,000 individuals were collected (Velasco 2008), confirmed the huge abundance and diversity of species, many of them being represented by only one or two individuals. Since 1993, a total of 168 species and 49 genera of butterflies from Ecuador have been described by various authors (see Willmott & Hall 2008, for a complete list of references). About 200 species and 8 genera still require formal description. Even for a relatively well-studied group like Papilionoidea, one highly distinctive and four cryptic undescribed species have been recognized since 1998, all occurring in Andean habitats (Jasinski 1998; Willmott *et al.* 2001). More poorly studied groups, such as the Lycaenidae, Riodinidae and Satyridae, are likely to contain even higher proportions of new or unrecognized species (Willmot & Hall 2008) suggesting that Ecuador remains a source of many discoveries for lepidopterists.

Regarding the Coleoptera of Ecuador, and particularly Carabidae, the most complete study is by P. Moret on the Carabidae of the Páramo in the Ecuadorian Andes (Moret 2005). The Páramos are mountain ecosystems consisting of large areas of herbaceous plants and sclerophylous shrubs, above the tree line (3400–3600 m) and below the permanent snowline (4800–5000 m, fig. 2B). Based on the direct examination of about 8500 individuals, Moret (2005) reviewed 16 genera and 204 species, of which 57 were new to science. The flightless condition of most (96%) high Andean Carabidae implies reduced dispersal ability and has led to a great number of geographically restricted species. The author considered a total of 191 species (94%) as micro - or meso-endemic to the Ecuador Andes. This rate of endemism is similar to that found in the Andes near Mérida, Venezuela (91%, Perrault 1994), although Ecuadorian Carabidae exhibit a higher diversity, both at specific and generic levels. Endemism rates are lower among the Alpine Carabidae of the Alps (60%, Brandmayr *et al.* 2003) and the Pyrenees (44%, Moret 2005) with a higher number of genera and fewer species in each genera.

These detailed works on the Papilionoidea and Carabidae reveal three main characteristic of the Ecuadorian entomological fauna which can be generalized to most taxonomic groups throughout the country: 1) the huge diversity of species in a great diversity of habitats, 2) the difficulty in identification of most species, and 3) the lack of published basic biological information, partly due to the high rate of endemism of many groups especially in the Andes (Table 1). For example, an exhaustive survey of stingless bees (Hymenoptera: Meliponinae) in 14 provinces of Ecuador by Coloma (1986) reported a total of 73 species, of which 13 were new species for science and 49 new records for Ecuador. Similarly, Ayala (1998) and Battiston & Picciau (2008) reported a total of 69 species of mantids (Mantodea) of which 10 were new to science. The high rate of endemism for many groups such as Coleoptera, especially in the Andean region, also complicates the work of taxonomists. For example, the Ecuadorian tiger beetle fauna (Coleoptera: Cicindelidae) contains 12 genera and 74 species, of which 26.0% are endemic (Nuñez *et al.* 1994; Pearson *et al.* 1999). This is the highest percent of endemism among all Andean countries (Nuñez *et al.* 1994). Similarly, 173 species of Dynastinae beetles (Coleoptera: Scarabeidae) have been reported in Ecuador, of which 35 are endemic, mainly from the genus *Cyclocephala* (Ortiz 1997). Finally, of the 283 species of Ecuadorian Rutelinae beetles, 26.8% are endemic (Paucar 1998; Smith 2003). The high rates of endemism observed for many insect groups (Table 1) represent a challenging issue for insect taxonomists not only in Ecuador but also in neighboring countries.

Agricultural entomology

The development of entomology as a scientific

Table 1. Diversity of species and genera and percentage of endemism of several taxonomic groups of insects in Ecuador.

Order	Taxonomic group	Number of species	Number of genera	Main genera (nb. species)	% endemism in Ecuador	References
Hymenoptera	Meliponinae	73	17	Trigona(20, Melipona(8)	31.1	Coloma (1986)
	Formicidae	670	74	*Pheidole* (93), *Camponotus* (58)	10.7	Donoso (unpubl. data)
	Ithomiinae	116	32	*Pteronymia* (15), *Oleria* (14)	43.0	Gil (2001)
Diptera	Tabanidae	204	33	*Tabanus* (40), *Esenbeckia* (16)	12.2	Cárdenas & Buestan (this issue)
	Drosophila	112	1	-	36.6	Acurio & Rafael (unpubl. data)
Orthoptera	Caelifera	216	117	*Jivarus* (15), *Orphulella* (6)	55.0	Buzzetti & Carotti (2008)
	Mantodea	63	37	*Vates* (5), *Acanthops* (4)	34.8	Ayala (1998), Battiston & Picciau (2008)
Isoptera	all	62	28	*Nasutitermes* (15), *Anoplotermes* (6)	-	Bahder et al. (this issue)
Coleoptera	Cicindelidae	74	12	Cicindela (26), Odontocheila (14)	29.2	Nuñez *et al.* 1994
	Dynastinae	173	40	Cyclocephala(67), Ancognata(13)	20.2	Ortiz 1997
	Rutelinae	283	38	*Platycoelia* (144), *Anomala* (64)	33.4	Paucar (1998), Smith (2003)
	Sacarabeinae	233	21	*Onthophagus* (31), *Canthidium* (25)	-	Carpio, unpubl. data
	Carabidae	377	83	*Dyscolus* (63), *Blennidus* (33)	40.8	Zapata (1997)

discipline in Ecuador has been fostered by demand-driven entomological research, especially research aimed at solving specific problems related to agriculture. Since the creation of the National Institute of Agronomical Research (INIAP, *http://www.iniap-ecuador.gov.ec*) in 1959, this research has focused on the study of deleterious effects of insect pests on local crop production, e.g. fruit fly (Molineros *et al.* 1992; Feican *et al.* 1999), white fly (Peralta 1993), potato weevil (Gallegos *et al.* 1997), potato tuber moths (Pollet *et al.* 2003) or on the development of agro-industrial projects such as cultivation of purple African nightshade (*Solanum marginatum,* Moya 1985) or African palm (*Elaeis guinensis*, Martinez 1991).

If diversity is a main feature of the entomological fauna in natural habitats, this is also true for cultivated landscapes (fig. 2D). For example, Onore & Arregui (1989) identified 27 insect pest species associated with *Lupinus mutabilis*, a species of lupine grown in the Andes for its edible bean. Of the 27 species, 13 were Lepidoptera (e.g. the noctuids *Copitarsia* sp., *Agrostris* sp., *Autoplusia* sp.) whose larvae feed on lupine leaves and seeds. Another major Andean crop, quinoa (*Chenopodium quinoa*), is attacked by at least 18 pest species, mainly lepidopteran Noctuidae (*Copitarsia* sp., *Agrostris* sp.) (Fiallos 1989). Balsa (*Ochroma pyramidale*), a large fast-growing tree that can grow up to 30 m, has 68 insect pests including 60 species of Lepidoptera, mainly Arctiidae and Saturniidae (Barragán 1997). Finally, sixteen defoliator species are associated with the UICN red-listed *Podocarpus oleifolius* (Podocarpaceae) of which 12 belong to the Geometridae (e.g. *Anisodes atrimacula*, *Sabulodes boliviana*) (Salazar 1998).

The origin and the implications of such pest diversity for agro-ecosystem productivity are virtually unknown. Whereas inter-specific competition may be a key factor limiting insect diversity and abundance on the same host plant, mutualistic mechanisms (such as resource partitioning, sequential attack of the host plant) can promote coexistence among species. For example, in a study on the lepidoteran larva community on *Podocarpus*, Salazar (1998) showed that some species are specialized on the apex of the needle-like leaves whereas others feed on edges or stems. Similarly, Mazoyer (2007) showed the existence of facilitation mechanisms among pairs of potato moth species (Gelechiidae). Some species increased their feeding rate and survival when the tuber had been first infested by another species. Insect diversity and abundance can also be shaped by predator communities; however the high diversity of insect predators in Ecuador makes this a complex issue. For example, Martinez (1991) reported that more than 50 species of parasitoids, mainly hymenopteran Chalcididae and Eulophidae and dipteran Tachinidae, were associated with 44 species of defoliators, mainly Limacodidae and Brassolidae Lepidopterans, in African palm (*Elaeis guinensis*) crops.

Ecological entomology

Because the complex patterns of uplift of the Andean cordillera and oceanic islands, a large number of speciation events took place in Ecuador. This makes this country not only a productive place for studies on insect taxonomy, but also on insect ecology, evolution, or biogeography (Peck 2001; Moret 2005; Jiggins *et al.* 2006). This unique environmental and evolutionary history has attracted a long list of explorers and naturalists such as Darwin, von Humboldt and Whymper who have played an important role in fostering an interest in South American natural history and evolution of insects (Barragán *et al.* this issue). Despite the biological diversity of Ecuador and the scientific interest it has generated in the past, the development of ecological entomology as a formal discipline in Ecuador is a very recent phenomenon. It has been mostly limited to descriptive studies on environmental factors that govern insect diversity and abundance in different types of natural habitats. Examples include the study of seasonality and stratification of butterfly and locust communities (DeVries *et al.* 1997; Amédégnato 2003; Checa 2006; Velasco 2008), the microdistribution of vector and pest insects (Suarez 2008; Dangles *et al.* 2008) or the altitudinal distribution of insect species (Brehm *et al.* 2003a, 2003b; Jacobsen 2004; Hilt & Fiedler 2006; Cárdenas 2007; Fiedler *et al.* 2008).

The succession of plant and animal communities along altitudinal gradients has been of major interest for ecologists, especially in temperate regions (Berner *et al.* 2004; Hodkinson 2005). More recently, a growing number of studies have investigated the diversity of insect assemblages along altitudinal gradients in species-rich tropical regions (Brühl *et al.* 1999; Axmacher *et al.* 2004), including Ecuador for several groups such as moths (Geometridae: Hilt & Fiedler 2006, Gelechiidae: Dangles *et al*. 2008) Dipteran Tabanidae (Cárdenas 2007), and aquatic insects (Jacobsen 2004). The works by Jacobsen on streams and rivers (fig. 2E) represent the most complete study ever realized in the country on the ecological and physiological factors that govern distribution patterns of insects along altitudinal gradients (Jacobsen *et al.* 1997; Jacobsen 1998; Jacobsen *et al.* 2003; Jacobsen 2008a). A combination of empirical and experimental studies has shown that distribution patterns correspond to the respiratory physiology of individual species in relation to the temperature and oxygen regime of the environment (Jacobsen & Brodersen 2008). Both temperature and oxygen saturation of stream water decrease with altitude. These two factors are highly correlated to the decrease in diversity of macroinvertebrates with altitude in Ecuadorian streams (Jacobsen 2008b). In addition, Rostgaard & Jacobsen (2005) showed that oxygen availability in streams is expected to decrease more with altitude than respiratory oxygen demand by macroinvertebrates, potentially affecting the composition of communities in streams at very high altitudes (Jacobsen *et al.* 2003). Orography of Ecuador should foster more studies on insect response to the changing environments experienced along altitudinal gradients, especially with regard to the growing awareness that these responses may serve as analogues for climate warming effects at a particular altitude over time.

Future challenges: Ecuadorian entomology in a changing world

Habitat fragmentation

Ecuadorian civilizations, as well as the great Peruvian empire of the Incas, have inhabited in the Ecuador for thousands of years. Since 1950, the population of Ecuador has experienced a five-fold increase. With 13,780,000 inhabitants (INEC 2008), Ecuador is one of the most densely populated country in South America (55 inhabitant/km²) resulting in strong pressure on many natural ecosystems (fig. 3). Because the coastal region and the inter-Andean valleys are the most hospitable to people, they are also the most degraded parts of the Ecuador, with less than 10 percent of their original natural habitat remaining (fig. 3, UICN & WWF 2000). Ecuador together with Honduras and El Salvador have suffered the highest rates of deforestation in Latin America between years 2000–2005 (≥ 1.5% decrease in forest area /year *sensu* FAO 2007) principally due to changes in land use. In the montane forests, agriculture, dams, and road building are the most significant threats. At higher altitudes, seasonal burning, grazing, agriculture, mining, and fuel wood collection have degraded the grasslands and scrublands of páramos. In the Amazon, disturbances mainly originate from and oil and gas companies that have constructed several roads for prospecting and

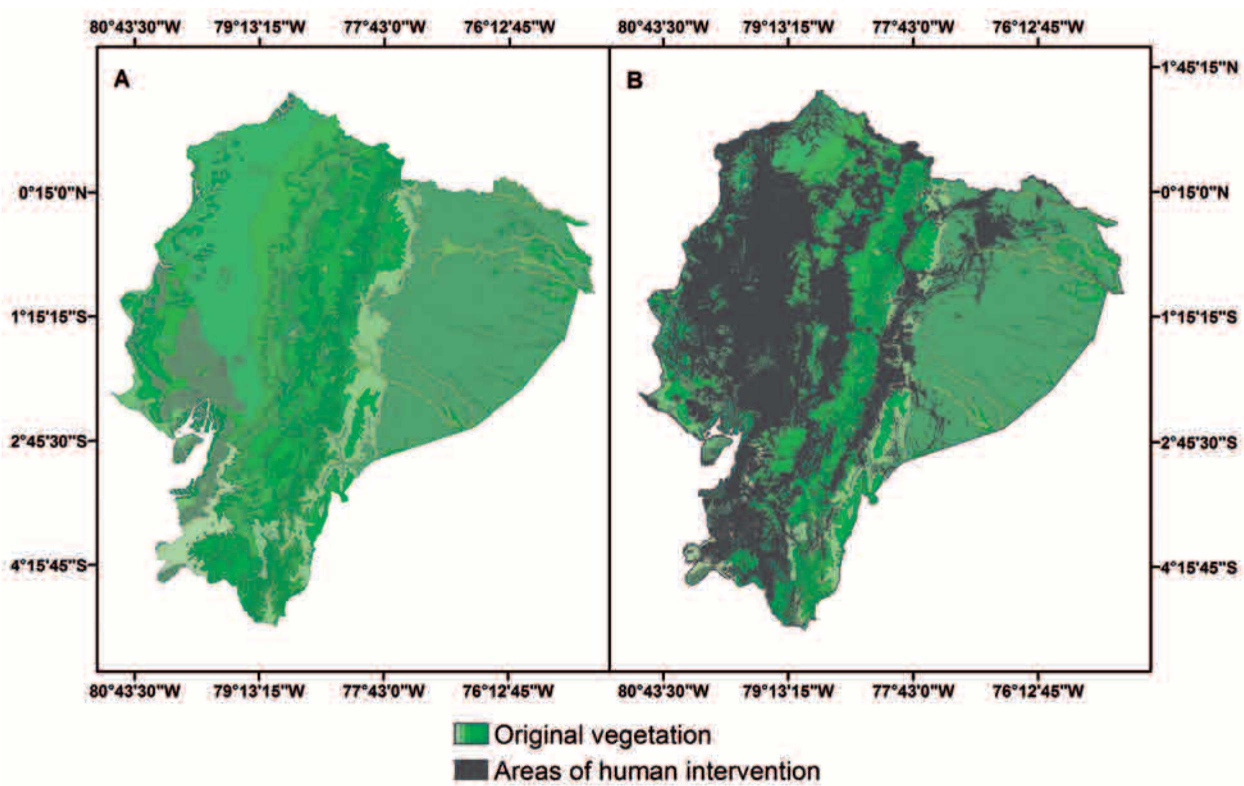


Figure 3
Maps of Ecuador showing (A) the original vegetation cover and (B) and the extent of habitat degradation in 2000, following Sierra (1999).

exploitation (Valencia *et al.* 2004). These roads have facilitated an extensive colonization by family farms and communities in previously unpopulated land. In the Galápagos, the introduction of domestic species such as goats, pigs, cats and rodents and the increase in bushfires frequency have deteriorated the natural vegetation of many islands. The clearing of native vegetation in the most humid zones for agriculture has significantly degraded the vegetation of the transition and scalesia zones on populated islands. This has been exacerbated by invasive plants such as raspberry (*Rubus niveus*), rose apple (*Syzygium jambos*), quinine (*Cinchona succirubra*), and Spanish flag (*Lantana camara*). Over 42.2% of the 438 exotic plant species are considered invasive (McMullen 1999).

Habitat fragmentation process implies habitat loss but also change in habitat configuration (Farhig 2003). While habitat loss has large, consistent negative effects on insect communities, habitat fragmentation *per se* has a much weaker effect, and may be negative but also often positive (Grez *et al.* 2004). In Ecuador, it has been shown that spatial scale affects significantly the response of insect communities to habitat fragmentation (e.g. Tylianakis *et al.* 2006 for cavity-nesting Hymenopterans on the Pacific Coast; Velasco 2008 for butterfly communities in the Chocó). The temporal component (time elapsed after disturbance) is also a crucial issue of habitat fragmentation (e.g. Abedrabbo 1988; Carpio *et al.* this issue). For example, Abredrabbo (1988) found a relatively fast recovery of terrestrial invertebrate fauna only 2 years after brush fires on Isabela Island, Galápagos. The rapid recolonization was facilitated by the presence of un-impacted isolated areas where the arthropod fauna was not altered. More studies separating the effect of habitat loss and fragmentation on insect communities, for example through manipulative experiments, are therefore urgently needed in Ecuador. Entomologists could also make good use of classical theories in community and population ecology such as the theory of island biogeography (McArthur & Wilson 1967), metapopulation dynamics (Levins 1969) and metacommunity dynamics (Holyoak *et al.* 2005) to predict the complex consequences of habitat fragmentation on the entomological fauna of Ecuador.

Climate change

Potential impact of climate change on the Ecuadorian fauna has been poorly explored and has been restricted to only a few groups such as Amphibians (Pounds *et al.* 2006; Ron *et al.* in press) or plants (DeVries 2006). Obviously, as is the case for all ectothermic organisms whose development time is temperature-dependent, insects are expected to respond strongly to changes in climate regimes, but this response may greatly differ depending on the region considered (Tewksbury *et al.* 2008). On the one hand, warming in the tropical Amazonian forest, although relatively small in magnitude, may have deleterious consequences because tropical insects are relatively sensitive to temperature change and may be living very close to their optimal temperature (Deutsch *et al.* 2008). On the other hand, effect of climate change on insect populations in the Andes is expected to be greater than in lowlands, reflecting the prediction of much larger proportional temperature rises in these areas (Hodkinson 2005). Warmer temperatures may affect population dynamics of some insect species (mainly agricultural pests), but also their altitudinal distribution. One of the few documented case in Ecuador is a study on the altitudinal distribution of the genus *Sphaenognathus* (Coleoptera: Lucanidae) (Onore & Bartolozzi 2008). Desiccated feces of lucanid larva were present in the soil at altitudes about 200 m lower than the lowest living populations of larvae at the time of their collections. This suggests an upward shift of these insects in the last 15–25 years. More studies on the impact of climate change on insects are definitely needed in Ecuador, especially because the small differences in elevation or vegetative cover over the country can create strong microclimatic differentials over short distances and allow development of persistent microclimatic refuges for insect populations to develop (see Dangles *et al.* 2008).

Invasive species

Although Andean countries have recognized the problems associated with invasive insect species for several years (Ojasti 2001), a comprehensive approach to this issue is still to be developed, especially in Ecuador. Globalization with expanding trade and increased human movement is likely to increase the risk of invasive insect species in South America. In the Andean region, commercial exchanges at regional and local scales have been the main causes for the rapid expansion of the potato tuber moth *Tecia solanivora*, (Lepidoptera: Gelechiidae), an exotic pest originating from Guatemala. This pest now represents one of the most serious agricultural pest problems in Ecuador (Puillandre *et al.* 2008). In the Galápagos Islands, a one-year survey of arthropod communities associated with agricultural areas on the Santa Cruz Island collected 160 species, of which 76 were introduced (e.g. the pyralid *Diaphania hyalinata*, Oquendo 2002).

Insect invasions can also spread and become established largely unnoticed as "tramp" species associated with human displacements. In a study of the drosophilid fly communities (Diptera: Drosophilidae) in Yasuni National park in the Amazonian rainforest, 7 of the 34 drosophilid species collected in habitats with various degrees of disturbance were exotic (Acurio *et al.*, pers. com.). A single study on Santa Cruz, Galápagos Islands, identified 17 ant species, of which only four were endemic and nearly all the rest were well-known tramp species (Clark *et al.* 1982).

New exotic host plants can also have indirect consequences for the native herbivorous insect fauna. Since its introduction in Ecuador in 1905, the Monterey pine (*Pinus radiata*) originating from California as well as the Mexican weeping pine *Pinus patula*, have been planted as large plantations (Woolfson 1987). The measuring worm (*Leuculopsis parvistrigata,* Lepidoptera: Geometridae), previously attacking *Hypericum laricifolium* and *Lupinus mutabilis*, was reported for the first time in 1980 attacking pine trees in Ecuador. Both direct and indirect consequences of invasion events for the structure and function of insect communities and the ecosystems they live in will be growing field of research for Ecuadorian entomologists.

Strategies for development of entomology in Ecuador

Priority research areas

To foster the development of entomology in Ecuador in the short term, it will be essential to support basic research while highlighting applied and demand-driven studies. We focus on three potential priority research areas although we are aware that many others could also be equally important.

Fostering the utility of entomological collections. The collection of the QCAZ contains more than 2 million specimens belonging to at least 30,000 taxa (see Donoso *et al.* this issue). In addition to taxonomic studies, it is important to diversify the use of this material towards other disciplines such as genomics and phylogenetics, morphology and development, population genetics, evolutionary ecology, conservation biology or even more distant fields such as pharmacology or biomimetics. Another key challenge will be to increase the availability of taxonomic and biological data on these species combined with detailed environmental data (e.g. Babin-Fenske *et al.* 2008; Foley *et al.* 2008). This could be achieved through digitizing the collection and the creation of databases available over the Internet. This will facilitate connections with foreign entomological collections and researchers. An effective collaboration of Ecuadorian entomological collections would significantly enhance their utility for international research programs and in return allow definition of new sampling strategies with regards to taxonomic groups and locations (see Graham *et al.* 2004). This process is currently underway but will demand continuous resources to be fully realized.

Insect diversity for ecosystem functioning. Decline of global insect diversity has recently focused attention on the implications of species losses for the maintenance of ecosystem functioning (Jonsson *et al.* 2002; Hoehn *et al.* 2008). In Ecuador, the functional relevance of the huge diversity of insects is virtually unknown. Functional diversity has been suggested to be the most important component of diversity (e.g. Tilman *et al.* 1997; Hulot *et al.* 2000) and a common approach to test the effects of biodiversity on ecosystem functioning is an experimental manipulation of functional guild diversity. This could be performed in Ecuador for a wide variety of groups and ecosystem processes such as butterflies and bees involved in pollination process or dung beetles and ants implicated in decomposition and nutrient cycling. Understanding the relationships between insect diversity and ecosystem functioning is crucial not only to predict the impact of the ongoing loss of Ecuadorian insects species but also to develop strategies to accelerate ecosystem restoration.

Entomology and the well-being of local people. Insects, such as agricultural pests or vectors of diseases, also put severe pressure on the well-being of millions of people in Ecuador. Both agricultural and medical entomology should be prioritized. The study of the entomological fauna of agro-ecosystems is particularly relevant in Ecuador where national parks and private biosphere reserves currently protect only about 20% of the land area, while cultivated area occupy almost half of the country (ECOLAP 2007, fig. 2D). Moreover, although a large proportion of Ecuadorian people is under the risk of insect-borne diseases such as Chagas' disease (30,000 persons), malaria (up to 12,000 persons during epidemic phases), onchocerciasis (up to 1,200 persons during epidemic phases), or dengue (up to 23,000 persons during epidemic phases) medical entomology in Ecuador is still in its infancy. Our knowledge is limited to a handful of studies on few taxa: *Rhodnius* spp. (Hemiptera: Reduviidae, Aguilar *et al.* 1999; Abad-Franch *et al.* 2005; Suarez 2008), *Anopheles* spp. (Diptera: Culicidae, Birnberg 2008) and *Simulium* spp. (Diptera: Simuliidae, Vieira *et al.* 2007). The development of national investigations for both areas of research (agronomic and medical entomology) is of major concern because many strategies for insect pest and insect vector management developed in other South American countries are not practical in Ecuador.

Increasing funding directed towards the study of insects

At present, limited national funding is one of the major obstacles to the development of entomology, as well as other life science disciplines in Ecuador. To increase the interest of policy makers for entomological studies, one possible approach is to enhance the awareness of the importance of the link between ecosystem health and human well-being, expressed in the context of ecological services. In this context, there is a vast diversity of insects involved in complex interactions that allow natural systems to provide ecological services on which humans depend (Losey & Vaughan 2006). Decomposition of organic matter, pest control, pollination, and food resource for wildlife are among the major processes accomplished by insects, allowing the global functioning of both natural and cultivated ecosystems (Samways 2005). In Ecuador, as well as in many parts of the world, these service-providing insects are under increasing threat from a combination of factors, including habitat destruction, invasion of foreign species, and overuse of toxic chemicals. Once the benefits of insect-provided services are realized, we hope to realize increased funding directed toward the study of insects and the vital services they provide so that conservation efforts can be optimized (Losey & Vaughan 2006).

Establishing monitoring networks

Monitoring is a fundamental part of environmental science and long-term data are particularly crucial for documenting key issues such as the spread of exotic species or the impact of climate change (Lovett *et al.* 2007). Monitoring networks also provide fundamental feedback for strengthening management and conservation programs and opportunities for increasing education and awareness (Martinez *et al.* 2006). In this context, insects have proven to be remarkable ecological sentinels for environmental changes in a wide range of tropical ecosystems such as forests (Basset *et al.* 2004), mountains (Moret 2005; Dangles *et al.* 2008) or rivers (Jacobsen 1998). Although the establishment of ecological networks with standardized, repeated, quantitative samplings faces limited funding and administrative capabilities in Ecuador, international initiatives could represent an opportunity for entomologists. For example, the Long-Term Ecological Research (LTER, *http://www.lternet.edu*) networks that have been established mainly for plant studies in various Latin American countries including Ecuador (Myster 2007) could also focus on the study of insect assemblages (Bashford *et al.* 2001). Another example is the Global Observation Initiative in Alpine environments (GLORIA, *http://www.gloria.ac.at*) whose purpose is to establish and maintain world-wide long-term observation networks in Alpine environments. Several sites have already been established in the Andes (Peru, Colombia, and Bolivia). Some of these include insect community monitoring. The Entomology Department of PUCE is currently involved in the establishment of a GLORIA site in Ecuador (Yanacocha Reserve, Province of Pichincha, Ecuador). Insect monitoring networks would also be a necessary tool for the surveillance of the dynamics of vector insects, e.g. Reduviidae (Abad-Franch *et al.* 2001) and agricultural pests, e.g. potato moth (Dangles & Carpio 2008).

Strengthening training and collaborations

Another important endeavor for the development of entomology in Ecuador will be to increase the small pool of trained entomologists. The lack of solid graduate programs in entomology and limited job opportunities push young professionals abroad, creating a serious "brain-drain" problem in the country. Efforts to develop local and regional entomological science should focus on retaining these valuable scientists, while continuing to foster international collaboration (see Martinez *et al.* 2006). To achieve this goal, it would be necessary to reduce the limitations that the bureaucracy of obtaining research and collection permits from the Ministry puts on researchers. This actually disencourages many potential work and collaborations, with both national and foreigner scientists. Any type of partnerships with foreign countries should be strengthened and promoted not only to provide unavailable expertise and techniques (e.g. molecular systematics, modeling) but also to increase the overall funding available for entomological research. Such collaborations must encourage Ecuadorian entomologists to publish their results in international peer-reviewed and indexed journals, so that the greatest amount of reliable scientific information on the taxonomy, distribution, ecology and evolution of entomological fauna of Ecuador can be available. This will help to ensure that entomological knowledge participates in promoting the conservation and sustainable use of the highly threatened natural resources of Ecuador.

Acknowledgements. The authors are grateful to Dean Jacobsen for valuable comments on an early version of the manuscript and to one anonymous reviewer for helpful comments on an earlier version of the manuscript.

References

Abad-Franch F., Paucar A., Carpio C., Cuba C.A.C., Aguilar H. M., Miles M. A. 2001. Biogeography of Triatominae (Hemiptera: Reduviidae) in Ecuador: implications for the design of control strategies. *Memórias do Instituto Oswaldo Cruz* **96:** 611-620.

Abad-Franch F., Palomeque F.S., Aguilar V.H.M., Miles M.A. 2005. Field ecology of sylvatic *Rhodnius* populations (Heteroptera, Triatominae): risk factors for palm tree infestation in western Ecuador. *Tropical Medicine and International Health* **10(12):** 1258-1266.

Abedrabbo S. 1988. *Efectos del incendio de 1985 sobre los invertebrados en Sierra Negra, Iisla Isabela, Galápagos.* Dissertation, Pontificia Universidad Católica del Ecuador, Quito, 232 p.

Aguilar H. M., Abad-Franch F., Racines J., Paucar A. 1999. Epidemiology of Chagas disease in Ecuador. A brief review. *Memórias do Instituto Oswald* **94:** 387-393.

Amédégnato, C. 2003. Microhabitat distribution of forest grasshoppers in the Amazon, p. 237-255 *in*: **Basset Y., Novotny V., Miller S.E., Kitching R.L. (eds)** *Arthropods of Tropical Forests. Spatio-temporal Dynamics and Resource Use in the Canopy.* Cambridge University Press, Cambridge.

Ayala M. 1998. *Los mántidos (Mantodea) del Ecuador: catálogo, distribución geográfica y notas de historia natural del género* Calopteromantis. Dissertation, Pontificia Universidad Católica del Ecuador, Quito, 184 p.

Axmacher J.C., Holtmann G., Scheuermann L., Brehm G., Müller-Hohenstein K., Fiedler K. 2004. Diversity of geometrid moths (Lepidoptera: Geometridae) along an afrotropical elevational rainforest transect. *Diversity and Distributions* **10:** 293–302.

Babin-Fenske J., Madhu A., Alarie Y. 2008. Rapid morphological change in stream beetle museum specimens correlates with climate change. *Ecological Entomology* **33:** 646-651.

Bahder B.W., Krecek J., Scheffrahn R.H., Keil C., Whitney-King S. 2009. Termites (Isoptera: Kalotermitidae, Rhinotermitidae, Termitidae) of Ecuador and the Galapagos Islands. *Annales de la Société entomologique de France* (n. s.) **45(4)**: 529-536.

Barragán A. 1997. *Plagas de la balsa (*Ochroma pyramidale*) (Cav. ex Lam.) Urban y sus controles naturales en una plantación forestal en la costa ecuatoriana.* Dissertation, Pontificia Universidad Católica del Ecuador, Quito, 157 p.

Barragán A., Dangles O., Cárdenas R., Onore G. 2009. History of Entomology in Ecuador. *Annales de la Société entomologique de France* (n. s.) **45(4)**: 410-423.

Bashford R., Taylor R., Driessen M., Doran N., Richardson A. 2001. Research on invertebrate assemblages at the Warra LTER site. *Tasforests* **13:** 109-118.

Basset Y., Mavoungou J.F., Mikissa J.B., Missa O., Miller S.E., Kitching R. L., Alonso A. 2004 Discriminatory power of different arthropod data sets for the biological monitoring of anthropogenic disturbance in tropical forests. *Biodiversity and Conservation* **13:** 709-732.

Battiston R., Picciau L. 2008. Contribution to the knowledge of the Mantodea of Ecuador with the description of the male of *Pseudoxyops perpulchra* (Westwood, 1889) (Mantodea, Mantidae Stagmatopterinae), p. 19-30 *in:* **Giachino P.M. (ed.),** *Biodiversity in South America I. Memoirs on Biodiversity World Biodiversity*, Association onlus, Verona.

Berner D., Körner C., Blanckenhorn W.U. 2004. Grasshopper populations across 2000 m of altitude: is there life history adaptation? *Ecography* **27:** 733-740.

Birnberg L. 2008. *Ecología y diversidad de* Anopheles *spp. en dos ecoregiones de la provincia de El Oro.* Dissertation, Pontificia Universidad Católica del Ecuador, Quito, 73 p.

Bollino M., Onore G. 2001. *Mariposas del Ecuador. Vol. 10 A. Papilionidae.* Pontificia Universidad Católica del Ecuador, Quito, 171 p.

Brandmayr P., Pizzoletto R., Scarlercio S. 2003. Diversity pattern of Carabidae in the Alps and the Apennines Nagy L., p. 306-317 *in:* **Nagy L., Grabherr G., Körner C., Thompson D.B.A. (eds.),** *Alpine biodiversity in Europe*. Ecological Studies 167, Heidelberg, Berlin.

Brehm G., Homeier J., Fiedler K. 2003a. Beta diversity of geometrid moths (Lepidoptera: Geometridae) in an Andean montane rainforest. *Diversity and Distributions* **9**: 351-366.

Brehm G., Sussenbach D., Fiedler K. 2003b. Unique elevational diversity patterns of geometrid moths in an Andean montane rainforest. *Ecography* **26**: 456-466.

Brühl C.A., Mohamed M., Linsenmair K.E. 1999. Altitudinal distribution of leaf litter ants along a transect in primary forest on Mount Kinabalu, Sabah, Malaysia. *Journal of Tropical Ecology* **15:** 265-277.

Buzzetti F.M., Carotti G. 2008. Annotated list of the *Caelifera* of Ecuador (Insecta: Orthoptera), p. 39-66 *in:* **Giachino P. M. (ed.),** *Biodiversity in South America I. Memoirs on Biodiversity World Biodiversity*, Association onlus, Verona.

Cardenas R. 2007. *Diversidad y ecología de Tabanidae (Diptera) en un bosque remanente del Chocó ecuatoriano*. Dissertation, Pontificia Universidad Católica del Ecuador, Quito, 157 p.

Cárdenas R., Buestan J., Navarrete R., Dangles O. 2009. Diversity and distribution notes of horse flies (Diptera: Tabanidae) from Ecuador: a review. *Annales de la Société entomologique de France* (n. s.) **45(4)**: 511-528.

Carpio C., Donoso D., Ramon G., Dangles O. 2009. Short term response of dung beetle communities to disturbance by road construction in the Ecuadorian Amazon. *Annales de la Société entomologique de France* (n. s.) **45(4)**: **XXX to be completed**.

Chaves J.A., Pollinger J.P., Smith T.B., LeBuhn G. 2007. The role of geography and ecology in shaping the phylogeography of the speckled hummingbird (*Adelomyia melanogenys*) in Ecuador. *Molecular Phylogenetics and Evolution* **43:** 795-807

Checa F. 2006. *Patrones de diversidad, fluctuaciones poblacional y correlaciones climáticas de comunidades de mariposas carroñeras (Lepidoptera: Nymphalidae) en la estacion cientifica Yasuni, Amazonia ecuatoriana.* Dissertation, Pontificia Universidad Católica del Ecuador, Quito, 107 p.

Clark D.B., Donoso C., de Villacis Y.P. 1982. The tramp ant *Wasmannia auropunctata*: autecology and effects on ant diversity and distribution on Santa Cruz Island, Galapagos. *Biotropica* **14:** 196-207.

Coloma L. 1986. *Contribución al conocimiento de las abejas sin aguijón (Meliponinae: Apidae: Hymenoptera) del Ecuador.* Dissertation, Pontificia Universidad Católica del Ecuador, Quito, 146 p.

Constant P. 2006. *Galapagos: A natural history guide.* Odyssey Books and Guides, Hong Kong, 213 p.

Dangles O., Carpio C. 2008. Cuando los científicos y las comunidades andinas unen sus esfuerzos para luchar en contra de una plaga invasora. *Nuestra Ciencia* **10:** 23-25.

Dangles O., Carpio C., Barragan A., Zeddam J.-L., Silvain J.-F. 2008. Temperature as a key driver of ecological sorting among invasive pest species in the tropical Andes. *Ecological Applications* **18(7):** 1795-1809

Deutsch C.A., Tewksbury J.J., Huey R.B., Sheldon K.S., Ghalambor C.K., Haak D.C., Martin P. R. 2008. Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Sciences* **105:** 6668-6672.

DeVries T. 2006. *Buddleja* está desapareciendo por culpa de *Pinus*, las plantaciones de pino y el cambio climatico ciambian el paramo. *Nuestra Ciencia* **8:** 15-18.

DeVries P.J., Murray D., Lande R. 1997. Species diversity in vertical, horizontal and temporal dimensions of fruit-feeding butterfly community in an Ecuadorian rainforest. *Biological Journal of the Linnean Society* **62:** 343-364.

Donoso D.A., Salazar F., Maza F., Cárdenas R.E., Dangles O. 2009. Diversity of insects in Ecuador: insights from type specimens at the Invertebrate Museum of the Catholic University of Ecuador (QCAZ). *Annales de la Société entomologique de France* (n. s.) **45(4)**: 437-454.

ECOLAP 2007. *Guía del patrimonio de áreas naturales protegidas del Ecuador*. Universidad San Francisco de Quito, Quito, 330 p.

Fahrig L. 2003. Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology and Systematics* **34:** 487-515.

FAO 2007. *Situación de los bosques del mundo. Parte 1: Progresos hacia la ordenación forestal sostenible. Capitulo América Latina y el Caribe*. Roma,143 p.

Feican M, Encalada A, Larriva C. 1999. Manejo integrado de las moscas de la fruta. *Revista Informativa del Instituto Nacional Autónomo de Investigaciones Agropecuarias* **86:** 1-54.

Fiallos E.A. 1989. *Entomofauna asociada a* Chenopodium quinoa *en las provincias de Imbabura, Pichincha, Cotopaxi y Chimborazo*. Dissertation, Pontificia Universidad Católica del Ecuador, Quito, 152 p.

Fiedler K., Brehm G., Hilt N., Süssenbach D., Häuser C.L. 2008. Variation of diversity patterns across moth families along a tropical altitudinal gradient in a tropical mountain ecosystem – a synthesis, p. 167-179 *in* **Beck E., Bendix J, Kottke I, Makeshin F., Mosandl R. (eds.)**, *Gradients in a Tropical Mountain Ecosystem of Ecuador*. Ecological Studies 198. Springer-Verlag, Berlin.

Foley D.H., Weitzman A.L., Miller S.E., Faran M.E., Rueda M.L., Richard C. 2008. The value of georeferenced collection records for predicting patterns of mosquito species richness and endemism in the Neotropics. *Ecological Entomology* **33:** 12-23.

Gallegos P., Avalos G., Castillo C. 1997. *El gusano blanco de la papa en Ecuador: comportamiento y control.* INIAP, Quito, Ecuador, 35 p.

Garzione C.N., Hoke G.D., Libarkin J.C., Withers S., MacFadden B., Eiler J., Ghosh P., Mulch A. 2008. Rise of the Andes. *Science* **320**: 1304-1307.

Gil J. 2001. *Distribución de Ithomiinae en el Ecuador.* Dissertation, Pontificia Universidad católica del Ecuador, Quito, 212 p.

Graham C.H., Ferrier S., Huettman F., Moritz C., Peterson A.T. 2004. New developments in museum-based informatics and applications in biodiversity analysis. *Trends in Ecology and Evolution* **19:** 497-503.

Grant P. 1999. *Ecology and evolution of the Darwin's finches*. Princeton University Press, Princeton, 512p.

Grez A. A., Zaviezo T., Reyes S. 2004. Short-term effects of habitat fragmentation on the abundance and species richness of beetles in experimental alfalfa microlandscapes. *Revista Chilena de Historia Natural* **77:** 547-558.

Guevara D., Iorio A., Piñas F., Onore G. 2002. *Butterflies and moth of Ecuador: Vol 17a Sphingidae*. Centro de Biodiversidad y Ambiente, PUCE, Quito, Ecuador.

Hilt N., Fiedler K. 2006. Arctiid moth ensembles along a successional gradient in the Ecuadorian montane rain forest zone: how different are subfamilies and tribes? *Journal of Biogeography* **33:** 108–120.

Hodkinson I.D. 2005. Terrestrial insects along elevation gradients: species and community response to altitude. *Biological Review* **80:** 489-513.

Hoehn P., Tscharntke T., Tylianakis J.M., Steffan-Dewenter I. 2008. Functional group diversity of bee pollinators increases crop yield. *Proceedings of the Royal Society of London B* **275:** 2283-2291.

Holyoak M., Leibold M.A., Holt R.D. 2005. *Metacommunities: spatial dynamics and ecological communities.* University of Chicago Press, Chicago, 503 p.

Hughes C., Eastwood R. 2006. Island radiation on a continental scale: exceptional rates of plant diversification after uplift of the Andes. *Proceedings of the National Academy of Sciences* **103:** 10334-10339.

Hulot F.D., Lacroix G., Lescher-Moutoue F.O., Loreau M. 2000. Functional diversity governs ecosystem response to nutrient enrichment. *Nature* **405:** 340-344.

INEC (Instituto Nacional de Estadisticas y Censos) 2008. *Ecuador en cifras*. Online version http://www.inec.gov.ec.

Jacobsen D. 2008b. Tropical high-altitude streams, p. 219-256 *in*: **Dudgeon D. (ed.)** *Aquatic Ecosystems: Tropical Stream Ecology.* Amsterdam.

Jacobsen D. 1998. Influence of organic pollution on the macroinvertebrate fauna of Ecuadorian highland streams. *Archiv für Hydrobiologie* **143:** 179-195.

Jacobsen D. 2004. Contrasting patterns in local and zonal family richness of stream invertebrates along an Andean altitudinal gradient. *Freshwater Biology* **49:** 1293-1305.

Jacobsen D. 2008a. Low oxygen pressure as a driving factor for the altitudinal decline in taxon richness of stream macroinvertebrates. *Oecologia* **154:** 795-807.

Jacobsen D., Schultz R., Encalada A. 1997. Structure and diversity of stream macroinvertebrates assemblages: the effect of temperature with altitude and latitude. *Freshwater Biology* **38:** 247-261.

Jacobsen D., Rostgaard S., Vásconez J.J. 2003. Are macroinvertebrates in high altitude streams affected by oxygen deficiency? *Freshwater Biology* **48:** 2025-2032.

Jacobsen D., Brodersen K.P. 2008. Are altitudinal limits of equatorial stream insects reflected in their respiratory performance? *Freshwater Biology* **53:** 2295-2308.

Jasinski A. 1998. Description of a new species of *Hypanartia* from southern Ecuador and northern Peru (Lepidoptera: Nymphalidae). *Genus* **9(3):** 405-410.

Jiggins C.D., Mallarino R., Willmott K.W., Bermingham E. 2006. The phylogenetic pattern of speciation and wing pattern change in neotropical *Ithomia* butterflies (Lepidoptera; Nymphalidae). *Evolution* **60:** 1454-1466.

Jonsson M., Dangles O., Malmqvist B., Guérold, F. 2002. Simulating species loss following disturbance: assessing the effects on process rates. *Proceedings of the Royal Society of London B* **269:** 1047-1052.

Kricher J. 2006. *Galapagos: A natural history.* Princeton University Press, Princeton, 256 p.

Levins R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America* **15:** 237-240.

Losey J.E., Vaughan M. 2006. The economic value of ecological services provided by insects. *Biosicence* **56:** 311-323.

Lovett G.M., Burns D.A., Driscoll C.T., Jenkins J.C., Mitchell M. J., Rustad L., Shanley J.B., Likens G.E., Haeuber R. 2007. Who needs environmental monitoring? *Frontiers in Ecology and the Environment* **5:** 253-260.

MacArthur R.H., Wilson E.O. 1967. *The theory of island biogeography.* Princeton University Press, Princeton, New Jersey, 203 p.

MacMullen C.K. 1999. *Flowering plants of the Galapagos.* Cornell University Press, Ithaca and London, 368 p.

Martínez E. 1991. *Defoliadores de la palma africana (*Elaeis guineensis *Jacq.) y sus controles naturales en una plantación industrial en la zona del Coca, Ecuador. Observaciones de polinización de* Jessenia bataua *(Arecaceae) en la Reserva de Producción Faunística Cuyabeno, Amazonía del Ecuador.* Dissertation, Pontificia Universidad Católica del Ecuador, Quito, 154 p.

Martinez M.L., Manson R.H., Balvanera P., Dirzo R., Soberon J., Garcia-Barrios L., Martinez-Ramos M., Moreno-Casasola P., Rosenzweig L., Sarukhan J. 2006. The evolution of ecology in Mexico: facing challenges and preparing for the future. *Frontiers in Ecology and the Environment* **5:** 259-267.

Mazoyer C. 2007. *Mécanismes d'interaction entre ravageurs invasifs tropicaux de la pomme de terre en Équateur.* MSc. Dissertation, University of Montpellier, France, 42p.

Molineros J., Tigrero J. O., Sandoval G. 1992. *Diagnostico de la situación actual del problema de las moscas de la fruta en el Ecuador.* Comisión Ecuatoriana de Energía Atómica, Dirección de Investigaciones, Quito, 53 p.

Moret P. 2005. *Los coleopteros Carabidae del páramo de los Andes del Ecuador. Sistematica, ecología y biogeografía.* Centro de Biodiversidad y Ambiente, Torino, Italia, 306 p.

Moya A. M. 1985. *Estudio del vector de mycoplasmas en Solanum marginatum.* Dissertation, Pontificia Universidad Católica del Ecuador, Quito, 118 p.

Myers N., Mittermeier R. A., Mittermeier C. G., Da Fonseca G. A. B., Kent J. 2000. Biodiversity hotspots for conservation priorities. *Nature* **403:** 853-858.

Myster R.W. 2007. Early successional pattern and process after sugarcane, banana, and pasture cultivation in Ecuador. *New Zealand Journal of Botany* **45:** 35-44.

Nuñez V., Onore G., Pearson D. L. 1994. Escarabajos tigre del Ecuador (Coleoptera: Cicindelidae), lista de especies y clave para géneros. *Revista de la Pontificia Universidad Católica del Ecuador* **13 (58)**: 57-67.

Ojasti J. 2001. *Estudio sobre el estado actual de las especies exóticas.* Biblioteca digital andina, Quito, Ecuador, 223 p.

Onore G., Arregui T. 1989. Estudio preliminar sobre la entomofauna asociada a *Lupinus mutabilis* Sweet, en el Ecuador. Memorias VI Congreso Internacional de Cultivos Andinos. INIAP, Quito.

Onore G., Bartolozzi L. 2008. Description of the larvae of *Sphaenognathus* (Chiasognathinus) *gaujoni* (Oberthür, 1885) and *S.* (C.) *xerophilus* Bartolozzi & Onore, 2006 (Coleoptera: Lucanidae), with observations about their altitudinal range extension, p. 399-406 *in:* **Giachino P. M. (ed.),** *Biodiversity in South America I. Memoirs on Biodiversity World Biodiversity*, Association onlus, Verona.

Oquendo R. 2002. *Invertebrados asociados a cultivos agrícolas de importancia económica en la isla Santa Cruz Galapagos.* Dissertation, Pontificia Universidad Católica del Ecuador, Quito, 120 p.

Ortiz P. 1997. Catálogo, biogeografía y notas de historia natural de los Dynastinae (Coleoptera: Scarabaeidae) del Ecuador. Dissertation, Pontificia Universidad católica del Ecuador, Quito, 323 p.

Paucar A. 1998. Rutelinae (Coleoptera: Scarabaeidae) del Ecuador: catálogo, zoogeografía y notas biológicas. Dissertation, Pontificia Universidad católica del Ecuador, Quito, 229 p.

Pearson D. L., Buestán J., Navarrete R. 1999. The tiger beetles of Ecuador: their identification, distribution and natural history. *Contributions on Entomology, International* **3:** 185-315.

Peck S. B. 2001. *Smaller orders of insects of the Galapagos Islands, Ecuador: Evolution, Ecology, and Diversity.* National Research Council, Research Press, Canada, 278 p.

Peralta E. 1993. Establecimiento del umbral de acción para el control de la mosca blanca (*Trialeurodes vaporariorum* W.) en frejol arbustivo en el valle del Chota - Imbabura – Ecuador. *Revista Informativa del Instituto Nacional Autonomo de Investigaciones Agropecuarias* **1:** 1-30.

Perrault G. G. 1994. Ecobiogeography of Carabidae in the Andes of Venezuela, p. 45-49 *in:* **Desender K., Dufrêne M., Loreau M., Luff, M. L., Maelfait J. P. (eds.)**, *Carabid beetles: Ecology and Evolution*, Series Entomologica 51, Kluwer Academia Publisher, Dordrecht.

Piñas F., Manzano I. 1997. *Mariposas del Ecuador. Vol. I. Géneros.* Quito, Pontificia Universidad Católica del Ecuador, 115 p.

Piñas F., Manzano I. 2003a. *Mariposas del Ecuador. Vol. 16a. Saturniidae.* Compañía de Jesús, Quito,79 p.

Piñas F., Manzano I. 2003b. *Mariposas del Ecuador. Vol. 21b. Arctiidae. Subfamilia: Ctenuchinae.* Compañía de Jesús, Quito, 97 p.

Pollet A., Barragan A., Zeddam J.-L., Lery X. 2003. *Tecia solanivora*, a serious biological invasion of potato cultures in South America. *International Pest Control* **45:** 139-144.

Pounds J.A., Bustamante M.R., Coloma L.A., Consuegra J.A., Fogden M. P. L., Foster P. N., La Marca E., Masters K. L., Merino-Viteri A., Puschendorf R., Ron S. R., Sánchez-Azofeifa G. A., Still C.J., Young B.E. 2006. Widespread amphibian extinctions from epidemic disease driven by global warming. *Nature* **439:** 161-167.

Puillandre N., Dupas S., Dangles O., Zeddam J. L., Capdevielle-Dulac C., Barbin K., Torres-Leguizamon M., Silvain J.-F. 2008. Genetic bottleneck in invasive species: the potato tuber moth adds to the list. *Biological Invasions* **10:** 319-333.

Ribas C. C., Moyle R. G., Miyaki C.Y. Cracraft J. 2007. The assembly of montane biotas: linking Andean tectonics and climatic oscillations to independent regimes of diversification in Pionus parrots. *Proceedings of the Royal Society of London B* **274:** 2399-2408.

Rostgaard S., Jacobsen D. 2005. Respiration rate of stream insects measured in situ along a large altitude range. *Hydrobiologia* **549:** 79-98.

Ron S. R., Guayasamín J. M., Coloma L. A., Menéndez-Guerrero P. A. (in press). Biodiversity and conservation status of Amphibians in Ecuador, *in*: **Heatwole H., Wilkinson J. W. (eds.),** *Amphibian Biology. Decline and conservation, Vol. IX.* Surrey Beatty & Sons Pty. Ltd. Australia.

Salazar F. 1998. *Lepidópteros defoliadores asociados a* Podocarpus. Dissertation, Pontificia Universidad Católica del Ecuador, Quito, 96 p.

Samways M. J. 2005. *Insect diversity conservation.* Cambridge University Press, Cambridge, 342 p.

Sierra R. (ed.). 1999. *Propuesta preliminar de un sistema de clasificación de vegetación para el Ecuador Continental*. Proyecto INEFAN / GEF-BIRF y EcoCiencia, Quito, Ecuador.

Smith A. B.T. 2003. A monographic revision of the genus *Platycoelia* Dejean (Coleoptera: Scarabaeidae: Rutelinae: Anoplognathini). *Bulletin of the University of Nebraska State Museum* **15:** 1-202.

Suárez M.V. 2008. *Ecología de Triatominos (Hemiptera: Reduviidae: Triatominae) peridomiciliares y silvestres en las provincias de Loja y Manabí.* Dissertation, Pontificia Universidad Católica del Ecuador, Quito, 96 p.

Tewksbury J., Huey R. B., Deutsch C. A. 2008. Putting the heat on tropical animals. *Science* **320:** 1296-1297.

Tilman D., Knops J., Wedin D., Reich P., Ritchie M., Siemann E. 1997. The influence of functional diversity and composition on ecosystem processes. *Science* **277:** 1300-1302.

Tylianakis J. M., Klein A.-M., Lozada T., Tscharntke T. 2006. Spatial scale of observation affects a, b and c diversity of cavity-nesting bees and wasps across a tropical land-use gradient. *Journal of Biogeography* **33:** 1295-1304.

UICN, WWF. 2000. Bosques nublados tropicales montanos: tiempo de acción. Suplemento especial del boletín arborvitae como complemento a la publicación del libro Decision Time for Cloud Forests de Bruijnzeel, L. A. & -Hamilton, L. S. 2000. Serie n°13, UNESCO.

Valencia R., Foster R. B., Villa G., Condit R., Svenning J.-C., Hernández C., Romoleroux K., Losos E., Magård E., Balslev H. 2004. Tree species distributions and local habitat variation in the Amazon: large forest plot in eastern Ecuador. *Journal of Ecology* **92 (2):** 214-229

Velasco N. 2008. *Patrones de diversidad de comunidades de mariposas carroñeras del Chocó ecuatoriano en bosque primario y intervenido.* Dissertation, Pontificia Universidad Católica del Ecuador, Quito, 63 p.

Vieira J. C., Cooper P. J., Lovato R., Mancero T., Rivera J., Proaño R., López A. A., Guderian R. H., Guzmán J. R. 2007. Impact of long-term treatment of onchocerciasis with ivermectin in Ecuador: potential for elimination of infection. *BMC Medicine* **5: 9**.

Willmott K. R., Hall J. P.W., Lamas G. 2001. Systematics of *Hypanartia* (Lepidoptera: Nymphalidae: Nymphalinae), with a test for speciation mechanisms in the Andes. *Systematic Entomology* **26(4):** 369-399.

Willmott K.R., Hall J.P.W. 2008. *Butterflies of Ecuador.* www.butterfliesofecuador.com /intro.html#state

Woolfson A.J. 1987. *Estudio de la biología de Leuculopsis parvistrigata (Lepidoptera, Geometridae), plaga de Pinus radiata.* Dissertation, Pontificia Universidad Católica del Ecuador, Quito, 64 p.

Zapata G. 1997. *Carabidae (Insecta: Coleoptera) del Ecuador: catálogo, notas biogeográficas y ecológicas.* Dissertation, Pontificia Universidad Católica del Ecuador, Quito, 237 p.