

Pastures vs forests: do traditional pastoral activities negatively affect biodiversity? The case of amphibians communities

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Abstract. Over centuries traditional pasturing created a complex landscape structure, but few studies have compared amphibian communities in traditional pasture with those in natural landscapes. In our study we assessed the impact of traditional pasture use in the Pyrenean region of Irati Forest. We also evaluated the relative importance of wetland and landscape features for amphibians. During 2010 and 2011, we monitored 45 wetlands and recorded for abiotic and biotic environmental variables and the features of the surrounding landscape. We recorded the occurrence of seven species of amphibians (*Calotriton asper*, *Salamandra salamandra*, *Lissotriton helveticus*, *Bufo bufo*, *Alytes obstetricans*, *Rana pyrenaica* and *Rana temporaria*); at least one amphibian was detected in 89% of wetlands. Both wetland and landscape features explained a significant amount variation of community structure. The composition of amphibian communities was strongly affected by the surrounding landscape, *S. salamandra* being associated with the most forested areas, while *B. bufo* and *C. asper* dominate the communities within pasture areas. Community richness was not significantly related to the cover of forest or to the pasture cover in the surrounding landscape. Furthermore richness did not peak at intermediate levels of forest cover or of the cover of pasture. Traditional pastoral activities do not reduce amphibian biodiversity compared to natural landscapes, and allow environmental heterogeneity that is needed for certain amphibians in mountain areas.

Key words: Grazing, agriculture, ecology, salamandra, management.

Introduction

Mountain landscapes have been managed by humans since millennia (Oliva & Gomez-Ortiz 2011). This resulted in a landscape that contains natural and culturally modified elements which harbor high biodiversity including species-rich plant communities (Negro et al. 2011, Fernandez-Gimenez & Estaque 2012). Transhumance (mobile pastoralism) is one of the oldest continuous systems of land use in Europe (Putzer 2012). As a product of this long history, in the Pyrenees and other European mountains the dynamics of biological communities and the patterns of pastoral land use are mutually dependent. Mountainous landscapes are undergoing sharp changes in recent years due to the abandonment of traditional practices, landuse intensification or land conversion (Bergmeier et al. 2010, Garbarino et al. 2011).

In the last decades, an increasing number of studies highlighted that freshwater biodiversity and communities can be strongly affected by the features of the surrounding terrestrial landscapes (Nardi et al. 2005, Bried & Ervin 2006, Denoël & Ficetola 2007, Lind et al. 2009, Manenti 2010, Ficetola et al. 2011a). Terrestrial environments play important roles in affecting the ecological features

of freshwater habitats. Upland vegetation can interact with geological and soil structure and deeply affect aquifer structure, water erosion and siltation (Dybkaer et al. 2012). Moreover, terrestrial ecosystems can provide a substantial subsidy of energy to freshwater habitats (Jansson et al. 2007). Pollution or alteration of terrestrial landscapes often has consequences on freshwaters, with important effects on aquatic and semiaquatic organisms living there (Warren et al. 2003). Several studies compared the patterns of terrestrial biodiversity between pastures and native forests (Soderstrom et al. 2001, Dorrough et al. 2012, Sullivan et al. 2012); conversely the effect of pastures on freshwater biodiversity is poorly studied. This happens especially in mountain regions where traditional grazing still occurs. Recent studies considering habitat features at the landscape scale revealed noteworthy differences between freshwater environments surrounded by open landscapes and those surrounded by increasing wood cover (Van Buskirk 2005, Gagné & Fahrig 2007, Werner et al. 2007, Ficetola et al. 2009, Ficetola et al. 2011a). In intensively grazed agricultural grasslands, pond biodiversity is often highly reduced with effects on both invertebrates and vertebrates (Silver & Vamosi 2012). For example, cattle grazing was as-

sociated with low crayfish populations in Australian streams, if compared with streams within native forest (March & Robson 2006). However low intensity (traditional) cattle grazing was associated with high biodiversity in European farmlands (Deckers et al. 2005, Dufour et al. 2006, Haslem & Bennett 2008, reviewed by Rosenthal et al. 2012).

Many amphibians are semiaquatic organisms which require freshwater habitats for breeding and larval development, while adults live in terrestrial environments. Landscape features can be important determinants of selection of amphibian breeding sites, and therefore amphibians can be useful to detect the effect of landscape modifications on freshwater biotopes (Skelly et al. 1999, Ficetola & De Bernardi 2004, Van Buskirk 2005). Furthermore, amphibians can play an important functional role in small wetlands, enhancing energy flow between terrestrial and aquatic ecosystems (Gibbons 2003, Hartel et al. 2010). Several species of Amphibians are associated with forests (Skelly 2004, Manenti et al. 2009), while others can exploit and colonize open landscapes (Skelly et al. 1999, Denoel & Ficetola 2008). Intensive pasturing may negatively impact amphibians through direct disturbance, alteration of environmental conditions and increased landscape homogenization (Ficetola et al. 2004, Denoel & Ficetola 2008, Bernarde & Macedo 2008, Curado et al. 2011). Actually, traditional rural landscapes may have high suitability for amphibians, particularly due to their wide, heterogeneous and unfragmented native vegetation covers (Hartel et al. 2010, Tanadini et al. 2012).

Landscape features may not be the only determinants of the structure of amphibian communities. Several wetland related features, particularly hydroperiod and predators may strongly affect breeding success and suitability of a waterbody for amphibians (Werner & Glennemeier 1999, Skelly et al. 2002, Werner et al. 2009). On the other hand, wetland features are linked to the surrounding landscapes by complex relationships (Allan 2004). Specific approaches are thus needed to tease apart the role of landscape and wetland features on amphibian communities (Ficetola et al. 2011a).

In this study, we analyzed the structure of amphibian communities in a traditionally managed pasture and a beech forest with old growth characteristics (the Irati Forest in Navarra – Spain). The aim of this study was two-fold. First, we evaluated the relative importance of wetland

and landscape features on the structure of amphibian communities. Second, we compared the richness and composition of amphibian communities across a gradient of landscapes, ranging from old growth forest to traditional pasture.

Materials and Methods

Study area

The study area is situated in the western Pyrenees between the southern Spanish side (Navarra) and the northern French side (Pyrenneés –Atlantique) and around the Irati Forest (lat: 42°59'.39"N long: 1°8'48.78" O). The Irati Forest is an ancient and protected native beech forest that extends 17,300 hectares mainly in the Spanish side. The forest is surrounded by grazing pastures. Pastures are situated between 500 and 2300 m a.s.l. They are still mainly communally managed. In Irati Forest, the pastoral activity at the higher altitudes is mostly of the "artzaia" type that is performed in mountains mainly during late spring and summer months (Caro 1971). Pastures are traditionally managed and characterized by seasonal cattle grazing. Transhumances are often short, and occur between the mountain pasture at the limit of Mediterranean slope and the winter pastures located in the piedmont. In spring and autumn, some sheep flocks are also allowed to graze these pastures and woods. Our research focused mainly around the Irabia Lake, on the central and western side of the Irati Forest, and westward the latter where other patches of beech forest occur, surrounded by extended pastures landscapes. Altitude of study wetlands ranged between 700 and 1200 m a.s.l.

Surveys and habitat characterization

We used both nocturnal and diurnal visual encounter surveys to evaluate the presence/absence of breeding adults, eggs or larvae of amphibians. To maximize the homogeneity of sampling among streams and pools, the same observer performed all surveys; for all sites, at least one visit was performed in daytime, and at least one visit was performed after dusk, using spotlights to lighten the stream. During each survey, we searched each pond along their shore or conducted a linear transect (of ca. 150 m) along streams. In some cases, we considered multiple sampling localities in the same stream, if environmental conditions (e.g., landscape, stream morphology) markedly changed along the stream course; the average distance between sampling localities within the same stream was 2140 m.

Damp biotopes were described on the basis of rapid bioassessment protocols (Barbour et al. 1999). We recorded four features describing wetland morphology, quality and ecosystem functioning, that can be important for the reproduction of amphibians. *i*) We distinguished between lotic (i.e. streams) and lentic (i.e. ponds) habitats; *ii*) we measured substrate heterogeneity on the basis of the percentage of alternation of substrate elements (sand, gravel, stones, sunken branches, see Petersen 1992). Each site was classified using the following rank scale: 1, ab-

sence of diversification, only a single substrate element covering almost 100% of the site; 2, poorly diversified, only 2 substrate elements covering >90% of the transect; 3, quite diversified, at least three elements present in at least 10% of the transect; 4, highly diversified, >90% of the transect presenting an alternation of at least three elements. Two parameters described the biotic features of sites: *iii*) fish presence / absence assessed by visual detection and *iv*) richness of macrobenthos community. Macrobenthos is often used as a measure of water quality, as polluted streams have poor macrobenthos communities (Maitland, 1990, Moss, 1998). We used a fine mesh net to collect macroinvertebrates along a linear transect. For 7 minutes we turned over the site substrate collecting the macrobenthos into the net. We divided it in systematic units (SU) as in the Extended Biotic Index protocol (Woodiwiss 1978), and for each site we recorded the maximum number of SU. Wetland features were recorded in the second visit to each wetland; we did not observe major modifications of features between the two visits performed to each wetland.

We also measured three variables representing the landscape surrounding each wetland: distance from forest and the percentage of wood and pasture cover within 100 m from each sampling point (Ficetola et al. 2009). Landscape variables were measured from the 1:25 000 SITNA vector map of Navarra (Geoportal de Navarra: <http://sitna.navarra.es/geoportal>) to measure wood cover and pasture percentage within 100 m, using the ArcView GIS 3.2 (© Esri, 1999). Preliminary analyses performed using a 400-m radius yielded nearly identical results (not shown).

Statistical analyses

A site is "occupied" if a species is detected at that site, but not detecting a species during sampling does not necessarily indicate its absence (MacKenzie 2006). We used Presence 2.4 (Hines 2006) to assess the detection probability of each species, assuming a constant detection probability across surveys. Preliminary analyses assuming survey-specific detection probability yielded similar results (not shown). We then calculated survey reliability as the probability of detecting a species after two surveys, following the formula in Gomez-Rodriguez et al. (2012)

We used a series of constrained redundancy analyses (RDA) to evaluate the relative role of wetland and landscape features on the multivariate structure (i.e. species composition) of amphibian communities. RDA is a canonical analysis, combining the proprieties of regression and ordination techniques, that allows evaluating how much of the variation of the structure of one dataset (e.g., community composition in a wetland; endogenous dataset) is explained by independent variables (e.g., habitat features; exogenous datasets) (Borcard et al. 2011). We considered two matrices of environmental features: wetland and landscape features; we used the matrix of species composition across as endogenous. To evaluate the independent role of landscape, we performed RDA assuming species composition as dependent, landscape as constraining matrix, and wetland features as conditioning matrix (the effect of which is partially out). Similarly, to

evaluate the independent role of wetland features, we used wetland features as constraining matrix, and landscape as conditioning. We also built an unconstrained RDA evaluating whether wetland features are significantly related to landscape features. We used variance partitioning to calculate the independent and joint effect of landscape and wetland features; we calculated the significance of explained variance by performing ANOVA-like permutation tests (10,000 permutations) (Borcard et al. 2011).

We used linear regression, assuming Poisson error distribution, to assess whether amphibian species richness significantly related to cover of forest or pasture in the surrounding landscape. Furthermore, to assess whether community richness peaks at intermediate levels of forest or pasture cover, we tested the significance of a quadratic term in regression models relating richness to landscape features. Due to overdispersion of data, in these models we used a quasi-Poisson family and tested significance using *F* tests (Crawley 2007). Prior to performing analyses, if necessary, environmental variables were transformed using logarithms (distance to forest) or square-root arcsine (forest and pasture cover). RDAs were computed on standardized variables using the vegan package (Oksanen et al. 2005); we performed all statistical analyses in R 2.14 (R Development Core Team 2012).

Results

Species distribution

We investigated 45 damp biotopes, and we recorded the breeding of at least a species of amphibian in 40 of them. We observed the breeding of 7 species: the fire salamander, *Salamandra salamandra* (occurrence, *O* = 38%); the Pyrenean brook salamander, *Calotriton asper* (*O* = 9%); the palmate newt, *Lissotriton helveticus* (*O* = 40%); the common toad, *Bufo bufo* (*O* = 22%); the midwife toad, *Alytes obstetricans* (*O* = 31%); the Pyrenean frog, *Rana pyrenaica* (*O* = 8.8%); and the common frog, *Rana temporaria* (*O* = 24.5%).

Rana pyrenaica was extremely localized; some of its records constitute the new range limit of the species (Manenti & Bianchi 2011). For all the study species, two surveys allowed us to assess absence with high reliability (Table 1).

Community analysis

Wetland and landscape features were significantly related among them (permutation test: *P* = 0.041). Landscape explained 18% of the variation of wetland features. Aquatic habitats from forests were more frequently lotic, showed rich macrobenthos communities and had high substrate heterogeneity (Fig. 1).

Amphibian community structure was signifi-

Table 1. Reliability of non-detection for the study species after two surveys without detection.

Species	Reliability
<i>Salamandra salamandra</i>	>0.99
<i>Calotriton asper</i>	0.96
<i>Lissotriton helveticus</i>	0.96
<i>Alytes obstetricans</i>	0.99
<i>Bufo bufo</i>	0.99
<i>Rana pyrenaica</i>	>0.99
<i>Rana temporaria</i>	>0.99

cantly related to both wetland and landscape features. The independent effect of landscape explained 17% of the variation of amphibian communities ($P < 0.0001$), while the independent effect of wetland features explained 20% of the variation ($P < 0.0001$). Furthermore, the joint effect of landscape and wetland explained 45% of community variation.

The relationships between wetland features and amphibian communities, when controlling for the potential effect of landscape, are shown in Fig. 2. *Lissotriton helveticus* was associated with lentic habitats with poor macrobenthos. On the contrary,

S. salamandra, *C. asper* and *B. bufo* were strongly associated with streams with rich macrobenthos and heterogeneous substrate. However, they selected different microhabitats, as *S. salamandra* avoided streams with fish occurrence, while *C. asper* and *B. bufo* were associated with streams with fish occurrence.

At the landscape level (Fig. 3), amphibians were distributed along a gradient between those living in forested landscapes, and those associated with wetlands embedded in pastures. *Salamandra salamandra* and, to a lesser extent, *R. temporaria* were associated with forested areas. *Lissotriton helveticus* was associated with intermediate forest cover, while *B. bufo*, *C. asper* and, at a lower degree, *R. pyrenaica* were associated open landscapes (i.e. pastures).

Overall, community richness was not significantly related to forest cover (Poisson linear regression: $F_{1,43} = 1.14$, $P = 0.29$) or to the cover of pasture ($F_{1,43} = 0.28$, $P = 0.60$) in the surrounding landscape. Furthermore, quadratic models suggest that species richness did not peak at intermediate levels of forest cover ($F_{1,42} = 0.001$, $P = 0.98$) or of the cover of pasture ($F_{1,42} = 0.060$, $P = 0.81$).

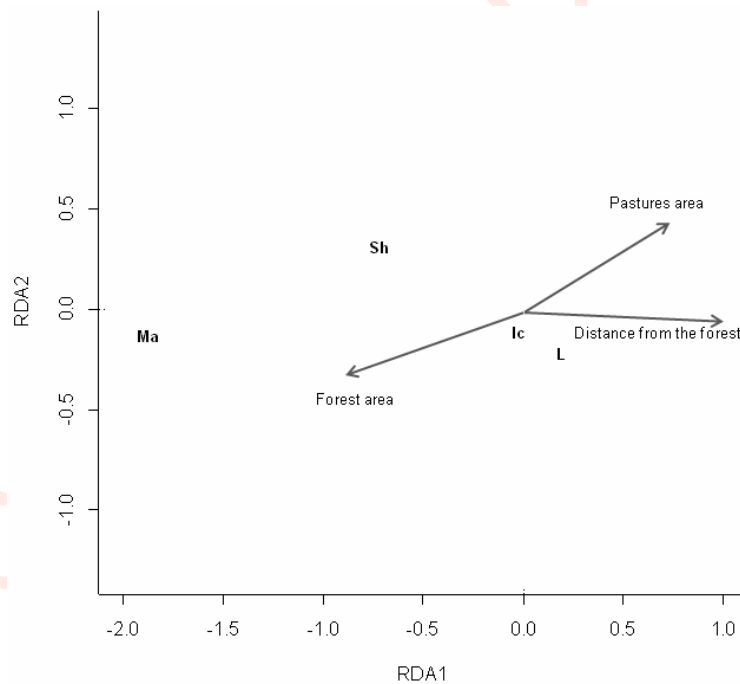


Figure 1. Results of constrained redundancy analysis showing the relationship between habitat and landscape features. Ma, Macrobenthos abundance, Sh, substrate heterogeneity, Ic, Ichtyofauna, L, lentic. Constraining variables are represented by grey arrows.

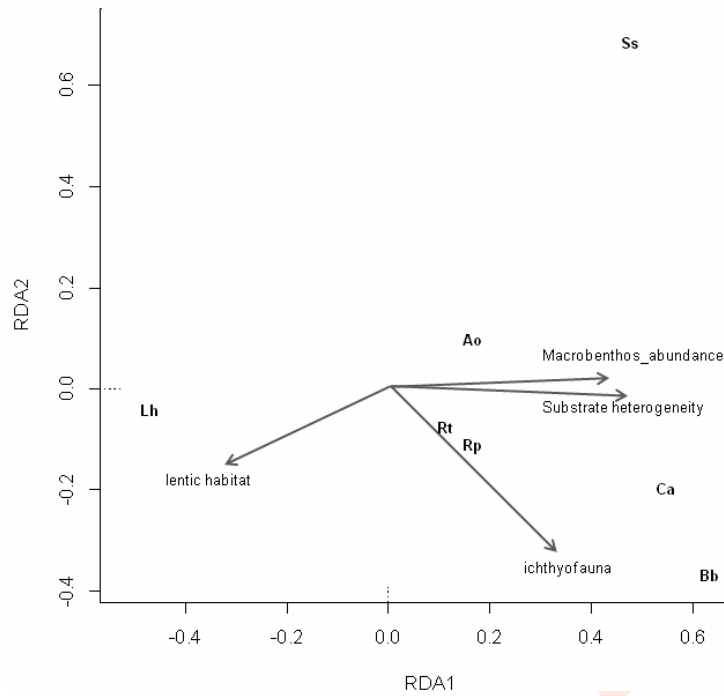


Figure 2. Results of constrained redundancy analysis showing the relationship between habitat features and amphibian distribution. Ss, *Salamandra salamandra*; Ca, *Calotriton asper*; Lh, *Lissotriton helveticus*; Ao, *Alytes obstetricans*, Bb, *Bufo bufo*; Rp, *Rana pyrenaica*; Rt, *R. temporaria*. Constraining variables are represented by grey arrows.

Discussion

Both landscape and wetland features strongly affected the distribution of breeding sites of most amphibians in the study area. The joint effect of wetlands and landscape explained more than 45% of the total amount of variation of community structure. Landscape and wetland features explained a similar amount of variation, suggesting that they have distinct but equally relevant roles in shaping amphibian communities. Among landscape features, the gradient between old growth forests and traditional pasture showed a non-trivial pattern: community richness was not highest in the most natural landscapes or in sites with intermediate cover of pasture. Instead, traditional pasture allowed relatively rich communities of certain amphibian species that are associated with open landscapes.

Among wetland features, there was a clear gradient ranging from lentic habitats with poor macrobenthos communities, and streams having rich macrobenthos and heterogeneous substrate (Fig. 2). Differences between lentic and lotic habi-

tats were a major determinant for *L. helveticus*, the only species that clearly selected ponds and pools. The association of *L. helveticus* to standing waters is known (Denoël & Lehmann 2006) and described also for other Pyrenean localities (Serra-Cobo et al. 1998) where it co-occurs also with *A. obstetricans* and *R. temporaria*. In our study, the association of common frog and midwife toad with lentic water was not confirmed, as they were weakly related to flowing waters. Even though *A. obstetricans* and *R. temporaria* often breed in ponds and pools (Pellet & Schmidt 2005, Gebremedhin et al. 2009), both species also breed in slow running watercourses (Nollert & Nollert 1992) and streams with suitable features are frequent in our study area. Three species are frequent in our study area. Three species are associated with lotic water: *S. salamandra*, *C. asper* and *B. bufo*. Among these, *S. salamandra* avoids streams with fish whereas the other two species, especially *B. bufo*, are associated withas observed in other study areas (Ficetola et al. 2011b). All of these species are related to watercourses with heterogeneous substrate and rich macrobenthos. Such relationships are not unexpected, as these two parameters are indicators of

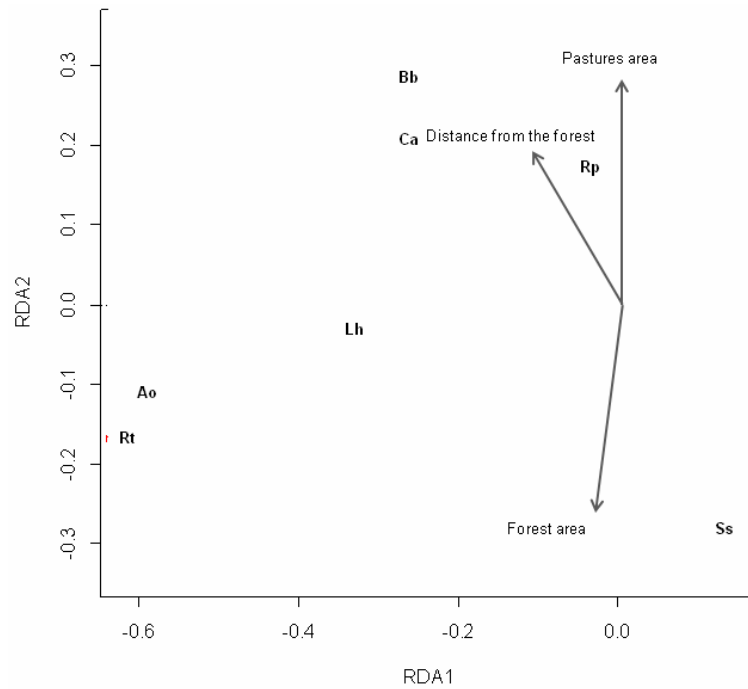


Figure 3. Results of constrained redundancy analysis showing the relationship between landscape features and amphibian distribution. Constraining variables are represented by grey arrows. See Fig. 2 for acronyms.

the shelters availability and water quality. For instance, *S. salamandra* typically inhabits highly diversified watercourses with rich macrobenthos, and these features are major determinants of its distribution (Manenti et al. 2009). Heterogeneous substrate may also enhance suitability for *C. asper*, for example by increasing shelter availability for eggs and larvae, especially if fish are present. Macrobenthos constitutes the primary prey of both adults and larvae of newts and salamanders, and rich macrobenthos communities are typically indicators of oligotrophic water (Koperski 2011). In other words, streams with rich macrobenthos likely have more food resources, and also less polluted water. Although the Pyrenean newt can prey on the tadpoles of some anurans (Serra-Cobo et al. 1998), those of *B. bufo* are unpalatable to most aquatic vertebrates. The toxicity of *B. bufo* tadpoles can thus allow the exploitation of streams with abundant predators such as *C. asper* and fish; in these streams toad tadpoles can avoid the competition of other amphibians that are more affected by predators (Van Buskirk 2003). The selection for similar habitats between *C. asper* and *B. bufo* has been also observed in other Pyrenean localities

(Serra-Cobo et al. 2000). Finally, *R. pyrenaica* occurred in very few sites: the study area is at the westernmost edge of its range (Manenti & Bianchi 2011) and is likely to represent the limit of its refugia during the last ice age (Gosá Oteiza et al. 2010). This frog is adapted to flowing waters (Serra-Cobo et al. 1998), but there are limited quantitative analyses on the habitat selection of this recently described species. Our results suggest that *R. pyrenaica* selects wetlands with habitat features similar to those selected by *R. temporaria* (Fig. 2), still, these two frog species co-occurred in only one pond, confirming early records of spatial segregation between them (Serra-Cobo et al. 2000).

At the landscape scale, one species (the fire salamander) was strongly associated with the most natural landscapes, as observed in other studies throughout Europe (Ficetola et al. 2009, Manenti et al. 2009, Ficetola et al. 2012). Other species, such as *R. temporaria*, *A. obstreticans* and *L. helveticus*, were located in landscapes with intermediate features, whereas two species (*B. bufo* and *C. asper*) were associated with more open areas, indicating that traditional pastures occurrence may be determinant for their distribution. Overall,

community richness was not significantly related to the cover of forest or to the cover of pasture in the surrounding landscape. Furthermore, richness did not peak at intermediate levels of these covers. In gradients of habitat degradation, species richness often peaks at intermediate levels of disturbance (intermediate disturbance hypothesis) (Connell 1978). However, for amphibian communities, a gradient is often observed between the forest- and open landscape-dependent species, and richness does not necessarily decline in the agricultural landscapes (Gagné & Fahrig 2007). Actually, traditional pasture can improve the suitability for certain amphibians through multiple mechanisms. First, several species are thermophilous, and have a limited fitness in closed canopy landscapes (Werner & Glennemeier 1999). Traditional pasture can allow the maintenance of the open landscapes that are needed for the most thermophilous species, without excessive anthropogenic impact. Furthermore, if compared with mechanized or intensive agricultural practices, traditional pasture allows the maintenance of small, semi-natural elements (e.g. pools for livestock watering, stone walls, ditch banks) that increase heterogeneity and provide suitable habitats for species that breed in open areas. Such positive role of pastures on biodiversity through habitat heterogeneity (such as, at the landscape level, the creation of more open areas and ecotones than in the original habitat, and at habitat level the higher shelter availability) has been recorded for other communities of both arthropods and vertebrates (Soderstrom et al. 2001, Moga et al. 2009, Negro et al. 2011). Traditional and not extensive pasture and agriculture practices can have positive effects on amphibian conservation, especially allowing the survival of the pools that are used for livestock watering or irrigation (Loman & Andersson 2007, Hartel et al. 2010, Tanadini et al. 2012, Romano et al. 2012).

The ecological context of our study area is particularly suitable to detect the role of pasture, because the traditionally conducted areas are nearby to highly extended and dense old growth forests. This is extremely different from what occurs in intensively grazed pastures, where the existence of habitats other than grassland is highly reduced (Silver & Vamosi 2012) and the loss and fragmentation of forests reduces the possibility of the landscape to support biodiversity (Kouba & Alados 2012). The differences in community structure of wetlands in forest and pasture highlights the im-

portance of considering biodiversity not only in terms of species richness, but also with respect to the distribution of each species. This is very important for amphibians, as species are adapted to a range of environmental conditions, and open, traditional landscapes do not necessarily support lower species richness (Gagné & Fahrig 2007). Our study suggests that conservation of traditional pastoral activities together with forest extension should be encouraged as a way of conserving the diversity of amphibians communities in mountain areas.

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Traditional pastoral activities and amphibian communities

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