

Influence of Landscape Elements in Riparian Buffers on the Conservation of Semiaquatic Amphibians

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Abstract: *Studies on riparian buffers have usually focused on the amount of land needed as habitat for the terrestrial life stages of semiaquatic species. Nevertheless, the landscape surrounding wetlands is also important for other key processes, such as dispersal and the dynamics of metapopulations. Multiple elements that influence these processes should therefore be considered in the delineation of buffers. We analyzed landscape elements (forest cover, density of roads, and hydrographic network) in concentric buffers to evaluate the scale at which they influence stream amphibians in 77 distinct landscapes. To evaluate whether our results could be generalized to other contexts, we determined whether they were consistent across the study areas. Amphibians required buffers of 100–400 m of suitable terrestrial habitat, but interspecific differences in the amount of habitat were large. The presence of amphibians was related to roads and the hydrographic network at larger spatial scales (300–1500 m), which suggests that wider buffers are needed with these elements. This pattern probably arose because these elements influence dispersal and metapopulation persistence, processes that occur at large spatial scales. Furthermore, in some cases, analyses performed on different sets of landscapes provided different results, which suggests caution should be used when conservation recommendations are applied to disparate areas. Establishment of riparian buffers should not be focused only on riparian habitat, but should take a landscape perspective because semiaquatic species use multiple elements for different functions. This approach can be complex because different landscape elements require different spatial extents. Nevertheless, a shift of attention toward the management of different elements at multiple spatial scales is necessary for the long-term persistence of populations.*

Keywords: community structure, forest, landscape composition, metapopulation, *Rana dalmatina*, *R. esculenta*, roads, riparian buffer, *Salamandra salamandra*, wetlands

Influencia de Elementos del Paisaje en Zonas de Amortiguamiento Ribereñas sobre la Conservación de Anfibios Semiacuáticos

Resumen: *Los estudios de zonas de amortiguamiento ribereñas generalmente se han enfocado en la cantidad de terreno requerido como hábitat para los estadios terrestres de especies semiacuáticas. Sin embargo, el paisaje que circunda a los humedales también es importante para otros procesos clave, como la dispersión y dinámica de las metapoblaciones. Por lo tanto, los múltiples elementos que influyen en esos procesos deberían ser considerados en la delineación de zonas de amortiguamiento. Analizamos los elementos del paisaje (cobertura forestal, densidad de caminos y red hidrográfica) en búferes concéntricos para evaluar la escala en la que influyen sobre anfibios de riachuelo en 77 paisajes diferentes. Para evaluar si nuestros resultados podían ser generalizados a otros contextos, determinamos si eran consistentes en las áreas de estudio. Los anfibios requirieron búferes de 100–400 m de hábitat terrestre adecuado, pero las diferencias interespecíficas en la cantidad de hábitat fueron grandes. La presencia de anfibios se relacionó con los caminos y la red hidrográfica en escalas espaciales mayores (300–1500 m), lo cual sugiere que se requieren búferes más amplios con esos*

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elementos. Este patrón probablemente surgió porque estos elementos influyen en la dispersión y la persistencia de la metapoblación, procesos que ocurren a escalas espaciales grandes. Más aun, en algunos casos, los análisis realizados sobre conjuntos de paisajes diferentes proporcionaron resultados diferentes, lo cual sugiere que se debe tener cautela cuando se aplican recomendaciones de conservación en áreas dispares. El establecimiento de zonas de amortiguamiento ribereñas no debería enfocarse solo en el hábitat ribereño, sino debe tener una perspectiva de paisaje porque las especies semiacuáticas utilizan múltiples elementos para funciones diferentes. Este enfoque puede ser complejo porque los diferentes elementos del paisaje requieren extensiones espaciales diferentes. Sin embargo, es necesario un cambio en la atención hacia el manejo de diferentes elementos a múltiples escalas espaciales para la persistencia de las poblaciones a largo plazo.

Palabras Clave: bosque, caminos, composición del paisaje, estructura de la comunidad, humedales, metapoblación, *Rana dalmatina*, *R. esculenta*, *Salamandra salamandra*, zona de amortiguamiento ribereña

Introduction

Semiaquatic species require complex combinations of terrestrial and aquatic habitat for their survival (Roe & Georges 2007). For this reason, in recent years there has been a growing interest in the delineation of riparian terrestrial buffers surrounding aquatic habitat. Buffer zones surrounding wetlands are frequently limited to a few tens of meters (Correll 2005). This corresponds to the amount of terrestrial habitat considered important for the conservation of water resources (Correll 2005). Nevertheless, recent analyses suggest that much larger areas can be needed for the conservation of semiaquatic species. Semlitsch and Bodie (2003) showed that at least 200–300 m of terrestrial habitat surrounding wetlands should be preserved to allow survival of terrestrial life stages of amphibians and reptiles.

The landscape surrounding wetlands can be used for several different functions, including dispersal, foraging, and overwintering. Furthermore, uplands are habitat for the terrestrial life stages (Olson et al. 2007). These functions can involve different life stages, and the extent of landscape required may differ for each. For example, many amphibian adults are philopatric and rarely move more than a few hundred meters from their breeding wetlands. These distances can be considered the amount of terrestrial habitat required (Berven & Grudzen 1990; Semlitsch & Bodie 2003, but see also Smith and Green [2005] for a critique on movement estimations). In many species dispersal is performed by juveniles and occurs over larger scales (Schroeder 1976; Berven & Grudzen 1990). Therefore, the buffers preserved as habitat for adults would not be sufficient for dispersal, which is necessary for linking different populations, allowing metapopulation persistence, and maintaining genetic diversity (Hanski & Gaggiotti 2004). Riparian buffers should allow for the multiple processes necessary for the long-term survival of populations. When critical processes occur over multiple spatial scales, this complexity should be considered in the delineation of buffers.

Two main approaches have been used for the delineation of buffer zones. First, the amount of terrestrial habitat is evaluated on the basis of data on animal movements and habitat use (e.g., Burke & Gibbons 1995; Semlitsch 1998; Bried & Ervin 2006; Crawford & Semlitsch 2007). Data obtained with techniques such as radiotracking, capture, and observations can be used for this purpose. Nevertheless, animal activities are frequently context dependent. The movements of a given species are strongly influenced by the features and quality of the surrounding landscape (Olden 2007; Olson et al. 2007). In unsuitable landscapes, movements can either be increased, to enhance the possibility of finding resources and new patches, or reduced, to avoid risks associated with the unsuitable matrix (Turcotte & Desrochers 2003; Bélisle 2005; Husté et al. 2006; Olden 2007). Therefore, despite the fact that data on animal movements provide useful insights, it is not clear to what level these results can be applied to different contexts, and generalizations can only be made when many studies are compared (e.g., Semlitsch & Bodie 2003).

The second approach compares species occurrence across different landscapes. Habitat variables are measured at different spatial scales, for example, in concentric buffers surrounding the wetlands. Species distribution is then related to environmental features at each scale. From this, it is possible to identify the scale at which species respond to landscape modifications, and management efforts can be focused at this scale (Vos & Stumpel 1996; Ficetola et al. 2004; Pellet et al. 2004). This indirect approach has an advantage over the first approach because it can be applied to large areas, but it is still difficult to evaluate whether the response to landscape features is constant (i.e., whether the critical amount of terrestrial habitat is the same across landscapes). Moreover, this approach does not involve the direct observation of animal activities; therefore, testing explicit hypotheses is necessary to evaluate whether different processes, such as dispersal, require the management of different spatial scales.

We used concentric analysis to evaluate the amount of landscape required by amphibian communities in small streams. Running waters are the breeding habitat of many amphibians, and riparian buffers play a key role in maintenance of stream conditions (Kiffney et al. 2003). Nevertheless, most studies on importance of buffers for amphibians have been performed on ponds (Olson et al. 2007). We investigated the landscape features that have key roles in 3 main processes: adult activity; dispersal and migration; and metapopulation persistence. In the study area, the adults of most of the amphibian species (e.g., *Salamandra salamandra*, *Rana dalmatina*, *R. latastei*) live in woodlands (Sindaco et al. 2006); therefore, we assumed that the amount of forest represents the terrestrial habitat. Roads are important barriers for amphibians because they cause mortality during migrations, hamper gene flow, and erode genetic diversity. Therefore, they are probably a key factor limiting dispersal and migration (Fahrig et al. 1995; Hitchings & Beebee 1997; Parris 2006; Ficetola et al. 2007a). Many amphibians survive in metapopulations or networks of patchy populations, and metapopulation theory predicts that the persistence of a population is favored by the presence of other nearby populations (Marsh & Trenham 2001; Hanski & Gaggiotti 2004). We therefore assumed that the density of wetlands plays a key role in the existence of these networks (Vos & Stumpel 1996; Ficetola & De Bernardi 2004). Finally, to evaluate whether the response to landscape features is constant across landscapes, we compared the results obtained in 2 distinct sets of landscapes. Our results shed light on the complexity of the delineation of buffers that allow the preservation of multiple processes.

Methods

Study Area and Design

To evaluate the effects of land alteration on species distribution, multiple landscapes should be compared. This approach, however, has been applied only rarely to amphibian studies (McGarigal & Cushman 2002; Cushman 2006). We analyzed 77 distinct habitat mosaics (hereafter landscapes) in a hilly area of Lombardy, northern Italy (Fig. 1). Human development in the study region is high,

and the road network is usually very dense. Nevertheless, several areas are protected within regional natural parks. For each landscape we recorded amphibian presence in a small watercourse, usually a first- or second-order stream. All streams were at similar elevations (200–570 m asl). Thirty-eight and 39 landscapes were investigated in 2004 and 2005, respectively (Fig. 1).

For the landscape surrounding each stream, we recorded 3 features on the basis of the Vector Map of Lombardy (www.cartografia.regione.lombardia.it): percent forest cover, length of the road network, and length of the hydrographic network. We used ArcView GIS (ESRI 1999) to measure each landscape feature within 16 concentric distances from the midpoint of the sampled streams: 50, 100, 200, 300, 400, 500, 600, 700, 800, 900, 1000, 1100, 1200, 1300, 1400, 1500 m. To ensure the distinctiveness of landscapes, each surveyed stream was >3000 m from the nearest sampling point; therefore, the measured buffers did not overlap.

Amphibian Surveys

We visited each stream at least 3 times from April to early June to evaluate amphibian presence. In each survey 2–3 observers evaluated amphibian presence with multiple techniques: visual transects along the water courses, repeated deep netting of the stream bottom, and funnel traps (Heyer et al. 1994; Olson et al. 1997). We placed the open side of the funnel traps (diameter 6 cm) facing the stream flow, mainly in pools. For each stream we placed 3 funnel traps in different pools and checked the traps after 7 days. A species was considered present if we recorded adults, egg masses, or larvae.

Data Analyses

We evaluated the effect of landscape composition at multiple scales on individual species, community richness (i.e., number of species), and community structure (i.e., species composition). We used generalized linear models (GLMs) to relate the distribution of individual species and the community richness to percentage of forest, road length, and length of the hydrographic network. We repeated analyses at each of 16 concentric buffers for which we measured landscape features. We used the amount of variation (deviance) explained by landscape

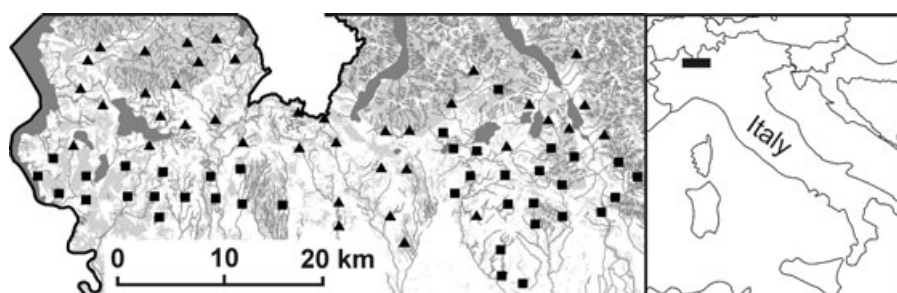


Figure 1. Study area maps and distribution of streams sampled for amphibians (squares, localities sampled in 2004; triangles, localities sampled in 2005; pale gray, forested areas; dark gray, hydrographic network).

features at each scale as a measure of the strength of the relationships. We then evaluated the spatial scale at which amphibian distribution was most strongly related to landscape by plotting the explained deviance against the radius of the measured buffer. We used a binomial error distribution for species presence and a Poisson error distribution for species richness. We evaluated the significance of relationships with a likelihood ratio test. When possible, to evaluate whether amphibian response is constant across landscapes (i.e., the possibility to generalize results to other contexts), we repeated this analysis with localities sampled only in 2004, localities sampled only in 2005, and with all localities pooled together.

Similarly, we used constrained redundancy analysis (RDA) to analyze community structure and to relate it to landscape features. An RDA is a canonical analysis combining the properties of ordination (e.g., principal component analysis) and regression techniques that allows one to evaluate how much of the variation of the structure of a multivariate data set is explained by independent variables (Legendre & Legendre 1998). As for GLMs, we evaluated relationships at the 16 concentric scales. We used amount of variation (inertia) explained as a measure of strength of the relationships. In RDA we calculated significance of relationships by performing a permutation test similar to analysis of variance (10,000 permutations) (Legendre & Legendre 1998). Some species were only observed during 1 sampling year. Therefore, we did not repeat RDA for the 2 separate years and only present results obtained by pooling the landscapes sampled during the 2 sampling seasons.

We used an information theoretic approach, on the basis of Akaike's information criterion (AIC; Burnham & Anderson 2002), to evaluate at which spatial scale landscape features affect species distribution. Per each model i , we calculated the AIC weight w_i and used the evidence ratios $E = w_i/w_j$ to compare relative support of the different plausible models i and j (Lukacs et al. 2007). This approach was applied when different analyses yielded discordant results on which scale had the strongest influence on amphibian distribution. When comparing 2 models, we assumed that a model had better support when the evidence ratio was >10 (Lukacs et al. 2007). Caution should be applied to the use of AIC-like methods in constrained ordination (Oksanen et al. 2005); thus, we did not calculate Akaike's weights for RDA.

Strong intercorrelation among different environmental variables (forest cover, length of road, and hydrographic network) can make interpretation of habitat models difficult. We therefore calculated the pairwise Pearson's correlations between the 3 landscape variables measured at all the considered scales (48 correlations evaluated). Hydrographic network length was not correlated to forest cover (for all correlations, $|r| \leq 0.2$, $p > 0.05$) or road length (for all correlations, $|r| \leq 0.3$; none of the correlations significant after Bonferroni's correction). We found

a moderate negative correlation between road length and forest cover at the largest spatial scales (at radii between 1000 and 1500 m, $-0.5 \geq r \geq -0.6$, all $p < 0.001$). This means that road density was lower in forested landscapes. Nevertheless, none of these scales were important for the analyses relating road density and forest cover to amphibian distribution (see Results); therefore, we assume these correlations had no major influence on our results. The pairwise correlation between forest cover and road length, measured at the 200–400 m radii, was $-0.25/-0.30$, and none of the pairwise correlations was significant after Bonferroni's correction.

Percentage data were transformed to the arcsine square root to meet the assumptions of parametric tests (Sokal & Rohlf 1995). We performed analyses with R 2.2 (www.r-project.org) and RDA with Vegan 1.6 (Oksanen et al. 2005).

Results

We observed 7 species of amphibians in the surveyed streams: fire salamanders (*S. salamandra*, occurrence = 45); smooth newts (*Triturus vulgaris*, occurrence = 1); green toads (*Bufo viridis*, occurrence = 2); common frogs (*R. temporaria*, occurrence = 2); agile frogs (*R. dalmatina*, occurrence = 9); Italian agile frogs (*R. latastei*, occurrence = 2), and pool frogs (*Rana synklepton esculenta*, occurrence = 10). The average number of species per stream was 0.92 (range: 0–3).

Species-Level Analyses

We performed the species-level analyses for the most common species, namely fire salamanders, agile frogs, and pool frogs. Only the fire salamander was observed in a large number of landscapes during both sampling years; therefore, we compared the 2004 and 2005 landscapes for this species only.

S. SALAMANDRA

The fire salamander was significantly and positively related to forest cover at all the recorded spatial scales. This species was most strongly related to forest cover within 100–400 m (Fig. 2), whereas the support of scales >600 m was low on the basis of AIC weights (Table 1; Supporting Information). When all landscapes were pooled together, the scale most strongly related to species distribution (hereafter the most likely scale) was 400 m, but the 100- to 300-m scales explained a similar amount of deviance and had similar AIC weights. Nevertheless, the results obtained over the 2 sampling years were quite different. For the landscapes sampled in 2004, the most likely scales were 300–400 m. On the basis of the evidence ratio, these scales were approximately 7 times

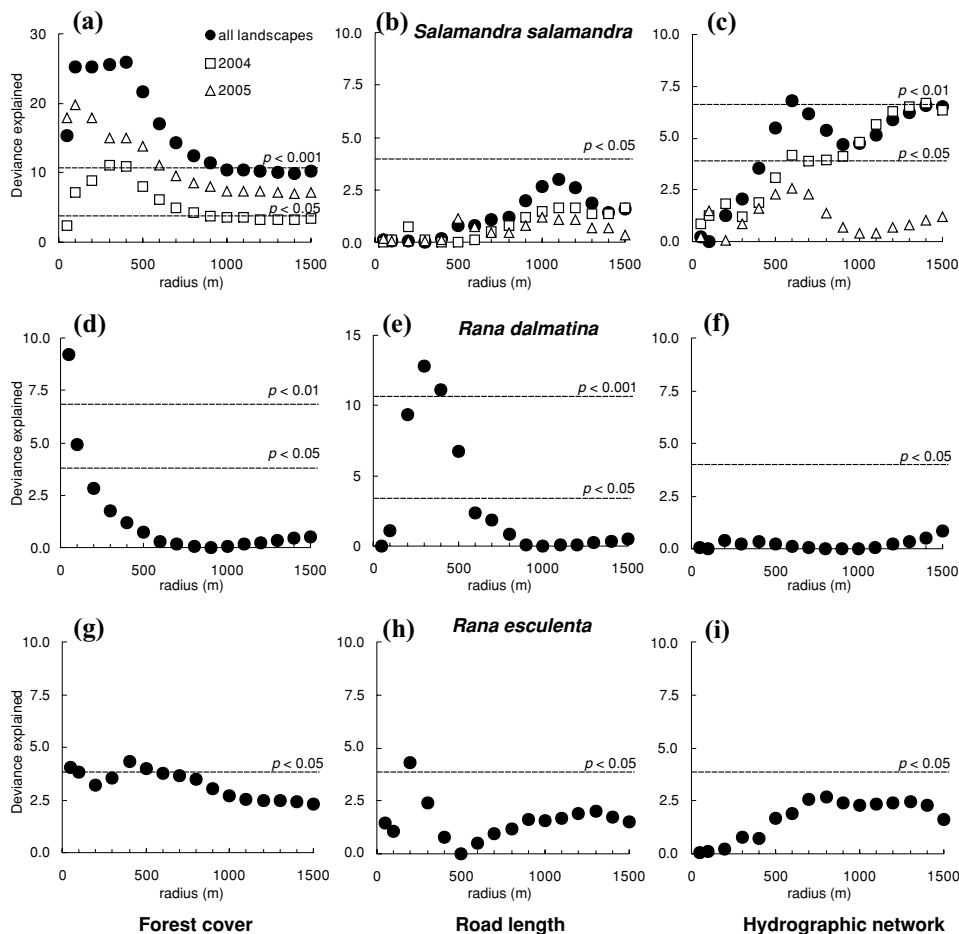


Figure 2. Strength of the relationships (measured using deviance) between the distribution of 3 amphibians and (a, d, g) forest cover, (b, e, h) road length, and (c, f, i) hydrographic network. Landscape features were measured at 16 buffers, with radius ranging from 50 to 1500 m (squares, relationships evaluated only for localities sampled in 2004; triangles, relationships evaluated only for localities sampled in 2005; circles, relationships evaluated by pooling all localities together). The ordinate axis is not the same for all panels. Points above the dashed lines indicate significant relationships.

more likely than the 100-m scale. Conversely, for the landscapes sampled in 2005, the most likely scale was 100 m; this scale was about 10 times more likely than the 300- to 400-m scales (Table 1).

The fire salamander was also positively related to length of the hydrographic network at scales >400 m. When all landscapes were pooled together, the most likely scale was 600 m (Fig. 2c); however, all scales from 500 to 1500 m had similar support (Table 1; Supporting Information). The most likely scale for landscapes sampled in 2004 was 1400 m, whereas it was 600 m for those landscapes sampled in 2005 (Fig. 2c), but the support did not differ strongly across scales. For example, in 2004 the 1400-m scale was only 3 times more likely than the 600-m scale.

R. DALMATINA

The agile frog was positively associated with forest cover at the smallest spatial scales (50–100 m). The relationship was particularly strong at 50 m. On the basis of the evidence ratio, the 50-m scale was 8.5 times more likely than the 100-m and 25 times more likely than the 200-m scales (Fig. 2; Table 1; Supporting Information). Moreover, the agile frog was negatively related to road

length within 200–500 m of the stream. This relationship was particularly strong at the 300-m spatial scale (Fig. 2). The agile frog was not significantly related to length of hydrographic network.

R. ESCULENTA

The relationship between pool frogs and forest cover was negative (i.e., this species was more frequent in the less-forested landscapes). This relationship was significant or close to significance at scales from 50 to 500 m; all these different scales were similarly supported. Moreover, the pool frog was negatively related to road length at the 200-m scale (Fig. 2; Table 1; Supporting Information). The pool frog was not significantly related to length of hydrographic network.

Community Analysis

Community richness was positively associated with forest cover at the 50- to 500-m spatial scale (Fig. 3). The scale with the highest support for community richness was 100 m. The effect of forest cover on community richness was similar during the 2 sampling years because 100 m was the scale with the highest support for both sets of landscapes (Fig. 3a). Relationships between the

Table 1. Akaike's weights of models relating amphibian distribution and landscape features, measured at different concentric buffers.*

	Spatial scale (m)															
	50	100	200	300	400	500	600	700	800	900	1000	1100	1200	1300	1400	1500
<i>Salamandrina salamandrina</i>																
forest cover	0.002	0.214	0.208	0.248	0.286	0.036	0.004	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
forest cover 2004	0.004	0.047	0.115	0.337	0.315	0.075	0.029	0.015	0.011	0.009	0.008	0.008	0.007	0.007	0.006	0.008
forest cover 2005	0.187	0.496	0.184	0.045	0.046	0.024	0.006	0.003	0.002	0.001	0.001	0.001	0.001	0.001	0.001	0.001
hydrograph network	0.005	0.004	0.008	0.012	0.026	0.069	0.134	0.099	0.066	0.046	0.048	0.058	0.086	0.102	0.120	0.117
hydrograph network 2004	0.009	0.011	0.014	0.010	0.015	0.027	0.046	0.040	0.042	0.045	0.064	0.097	0.132	0.151	0.161	0.136
hydrograph network 2005	0.037	0.071	0.034	0.051	0.073	0.103	0.120	0.104	0.066	0.047	0.041	0.040	0.046	0.050	0.055	0.061
<i>Rana dalmatina</i>																
forest cover	0.753	0.089	0.031	0.018	0.014	0.011	0.009	0.008	0.008	0.008	0.008	0.008	0.008	0.009	0.009	0.010
road length	0.001	0.002	0.104	0.589	0.262	0.028	0.003	0.002	0.002	0.001	0.001	0.001	0.001	0.001	0.001	0.001
<i>Rana esculenta</i>																
forest cover	0.089	0.080	0.059	0.068	0.102	0.087	0.077	0.073	0.067	0.053	0.045	0.042	0.041	0.041	0.040	0.038
road length	0.052	0.043	0.217	0.084	0.038	0.026	0.033	0.041	0.046	0.057	0.056	0.060	0.066	0.069	0.060	0.054

*Only landscape features for which the relationship was significant at least at one spatial scale are considered here. See Supporting Information for additional information on the models, including weights, number of parameters, and delta-AIC for all models.

other landscape features and community richness were not significant (Fig. 3).

The first component extracted by RDA explained 49.7% of the variance for community structure and indicated a gradient from communities dominated by *S. salamandrina* and *R. dalmatina* to communities dominated by *R. esculenta*. Community structure was significantly related to forest cover at all spatial scales; scales from 100 to 400 m explained the largest amount of variation (Fig. 3). Community structure was also significantly related to the hydrographic network in the 500- to the 1500-m scales; all these scales explained a similar amount of variation (Fig. 3).

Discussion

We analyzed concentric landscapes to identify at which scale semiaquatic species respond most strongly to habitat modifications. Nevertheless, our analyses also revealed the complexity of identifying these buffers. First, different species sometimes responded to landscape modification at different scales. Second, comparison of results obtained by the separate analyses of different sets of landscapes can be important in identification of patterns with high generality. Third, different landscape features influenced species at different scales, and this was probably caused by the functional role of the landscape elements.

Interspecific Differences

The species we analyzed separately (fire salamander, agile frog, and pool frog) showed different responses to landscape alteration, both for which elements are the most important and for the scales at which species respond (Fig. 2). For example, forest was positively related to salamanders and agile frogs, but negatively related to pool frogs. Interspecific differences in habitat requirement obviously play a major role in differences in response to habitat elements. For instance, woodlands are the main terrestrial habitat of several amphibians, including the fire salamander and the agile frog (Sindaco et al. 2006). This is also shown by the strong, positive effect of forest cover on community richness (Fig. 3a). Conversely, pool frogs are very adaptable, but are often associated with sunny wetlands in open landscapes (Ficetola & De Bernardi 2004; Van Buskirk 2005). This shift from communities dominated by forest specialists to communities dominated by the adaptable pool frog is well represented by RDA, which shows that forest cover is the main driver of community structure (Fig. 3). Species sharing similar requirements and vagility might be grouped in a community analysis to facilitate the definition of buffers, but this is an impossible task when heterogeneity among

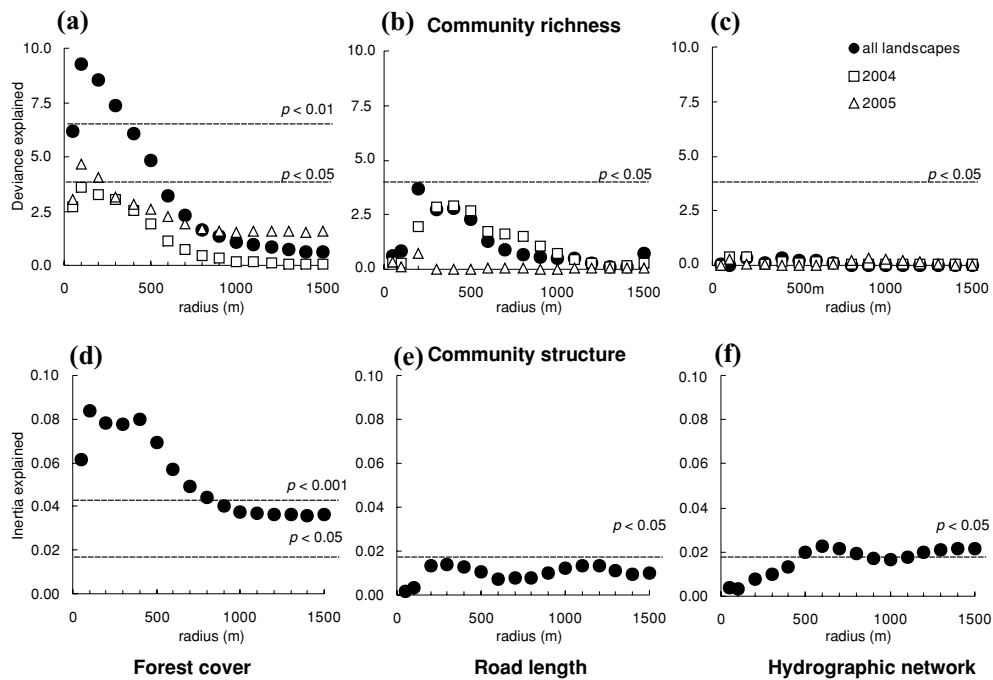


Figure 3. Strength of the relationships (measured using deviance or inertia) of (a–c) community richness and (d–f) community structure with forest cover, road length, and hydrographic network. Landscape features were measured at 16 buffers with radius ranging from 50 to 1500 m (squares, evaluated only for localities sampled in 2004; triangles, evaluated only for localities sampled in 2005; circles, evaluated by pooling all localities together). The significance of the relationships between landscape variables and community structure was evaluated with permutation tests; therefore, asymptotic values are not available, but all points above the dashed lines represent significant relationships.

species is strong. Instead, interspecific differences, such as those we observed, force conservation to target individual species according to conservation priorities and feasibility (Ficetola et al. 2007b; Denoël & Ficetola 2008).

Although 2 species may be related to the same landscape features, the extent of the habitat required may vary. For example, for the agile frog, 50 m was clearly the most likely scale for forest cover, whereas the fire salamander required much larger habitats because 400 m was the most likely scale. Evidence ratios constitute an objective measure of these differences in requirements (Table 1). The 50-m scale was 54 times more likely than the 400-m scale for the agile frog, whereas the 400-m scale was 143 times more likely than the 50-m scale for the salamander. Differences in the extent of required habitat are frequently related to species mobility because more mobile species are assumed to require larger habitat extents (e.g., Semlitsch & Bodie 2003; Denoël & Ficetola 2007; Olden 2007). Surprisingly, the existing data on the mobility of fire salamander do not confirm this pattern. The reported terrestrial movements are 300–500 m for the agile frog (Ponsero & Joly 1998; Stuempel 2005). These movements tend to be smaller for the salamander,

with maximum records of 200–500 m (July 1968; Denoël 1996; Schulte et al. 2007). Therefore, radiotracking and mark-recapture data do not suggest the fire salamander requires larger buffers than the agile frog.

It is not easy to explain the discrepancy between our analysis and more direct observations. It is possible that the 2 species have different susceptibility to negative edge effects (Schlaepfer & Gavin 2001) or have different tolerance to open habitats. Independent of the reason for this discrepancy, we believe it is urgent to cross-validate the results obtained by landscape analyses and direct observation. On one hand, results of landscape studies might be more reliable because presence data represent vital populations (we observed reproduction of salamander and agile frog in all landscapes where these species were present), whereas direct observation only provides a snapshot of the life of a few individuals. On the other hand, a landscape analysis is an indirect measure of requirements and does not evaluate actual habitat use. Complex interactions among species and landscape elements might thus affect patterns observed. We believe that it will be important to integrate the 2 approaches and compare the results obtained with different methods in the same area.

Generality of Riparian Buffers

A key question in habitat association studies is whether observed patterns can be generalized to other contexts (Menéndez & Thomas 2006; Whittingham et al. 2007). This question arises because the generality of relationships is a necessary prerequisite for their practical application to conservation planning (Whittingham et al. 2007). The context dependency of movements probably strongly affects the results obtained in studies of a single area. For this reason, we tried to maximize the number and independency of the studied landscapes. To our knowledge, we are the first to evaluate the generality of riparian buffers by comparing 2 sets of landscapes sampled during different periods.

In a few cases we observed moderate differences between the 2 sets of landscapes. For instance, the most likely scale for the relationship between forest cover and fire salamander was not identical for the 2 subsets (Fig. 2). Differences can arise when interactions between species and habitat are not constant across the landscapes. For example, the localities sampled in 2005 were at slightly higher elevations than those sampled in 2004 (mean [SD]: 2004, 317 m [78]; 2005, 360 m [99]). Forests at higher elevation may have differences in composition, undergrowth, and habitat quality, which might influence habitat use and movement (Bélisle 2005). These effects should be considered when translating conservation recommendations into new geographic areas. Despite small differences, the overall pattern remained the same across the 2 sets of landscapes (Table 1), and the results were very robust for the community analysis (Fig. 3). This suggests a good generality of patterns observed, particularly when the overall community is the target. Management recommendations obtained from these patterns are probably robust. Generality was remarkable also for the relationships among different landscape elements. In both years and in all the analyses, the elements influencing dispersal and metapopulations were related to species distribution at larger scales than the element that described habitat.

Different Buffers for Different Features

A striking result of our study is that when a species was influenced by multiple landscape elements, the most likely scale differed between elements. In almost all cases, terrestrial habitat (i.e., forest cover) influenced species at a smaller spatial scale than the elements that influenced dispersal and metapopulation persistence (i.e., roads and hydrographic network). This probably reflects the differences between the spatial patterns of habitat requirement and dispersion. The spatial scales of 50–400 m encompass the requirements of terrestrial habitat, and our analysis provided values for buffers similar to those proposed for amphibians on the basis of direct observation of life zone (Semlitsch 1998; Bulger et al. 2003; Semlitsch & Bodie 2003; Crawford & Semlitsch 2007).

Larger scales are important when examining road density and hydrographic network. In amphibian populations, long-range dispersers are infrequent but almost universally present (Smith & Green 2005), and they constitute the key for colonization of new habitats, gene flow among populations, and maintenance of (meta)population networks. Despite long-range dispersers being difficult to detect directly, population genetics provides compelling evidence of their role (e.g., Rowe & Beebe 2007). For these reasons maintenance of terrestrial habitat is not enough for long-term persistence of amphibians, and the landscape management needs to take into account the elements that allow dispersal and maintenance of population networks. The delineation of terrestrial habitat buffers should be followed by definition of larger areas of the landscape where protection can be less strict, but wetland persistence and road development should be carefully managed.

Conclusions: from Buffers of Habitat to Buffers of Landscape

A shift is occurring in conservation paradigms for semi-aquatic species. The recognition that terrestrial habitat is vital for semiaquatic species (Gibbons 2003) implies that conservation focusing only on aquatic habitats is not enough and large terrestrial buffers are needed for terrestrial life stages (Burke & Gibbons 1995; Semlitsch 1998; Bried & Ervin 2006; Crawford & Semlitsch 2007; Denoël & Ficetola 2008). Furthermore, different life stages require different landscape components, and permeable corridors are needed for maintenance of (meta)population processes. Therefore, a landscape-based approach should expand on the habitat approach (Joyal et al. 2001; Cushman 2006; Roe & Georges 2007). Our results stress the importance of incorporating different functions in the buffers surrounding wetlands (i.e., incorporating multiple landscape elements; Roe & Georges 2007). This means the focus needs to shift from “buffers of core habitat” to “buffers of landscape.” Even the management of nonterrestrial features (e.g., hydrographic network) should be planned in conjunction with the other elements, such as forests and roads.

Implementation of this approach can be complex because multiple features must be considered at the same time. A major issue for conservation practice is that different elements can require different spatial scales. Therefore, it is impossible to provide a single, always-valid measure. Focusing on the landscape element requiring the largest scale is a possible approach, but this would require very large buffers, and their application would not always be possible, especially in already modified areas. There may be an exciting role for landscape anisotropy in the management of features requiring different scales. The ease of species' movements can vary among different

axes of landscapes (Bélisle 2005; Olden 2007). Therefore, some landscape elements require large spatial scales, but only along preferential directions. For example, roads can have negative effects when they interrupt migration routes, whereas they may have lesser effects if they run parallel to those same routes. To date, the role of anisotropy has been poorly studied (Olden 2007), but it might be a key for successful management and deserves further in-depth investigation in the future.

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Supporting Information

Additional information on the models relating amphibian distribution and landscape features (Appendix S1) is available as part of the on-line article. The author is responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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