Nature Conservation 1: 53–71 (2012)
doi: 10.3897/natureconservation.1.2086
www.pensoft.net/journals/natureconservation

RESEARCH ARTICLE

A peer-reviewed open-access journal
Nature Conservation
Launched to accelerate biodiversity conservation

Road effects on habitat richness of the Greek Natura 2000 network

Nefta-Eleftheria Votsi[1], Antonios D. Mazaris[1], Athanasios S. Kallimanis[2], Maria S. Zomeni[3], Ioannis N. Vogiatzakis[3], Stefanos P. Sgardelis[1], John D. Pantis[1]

1 *Department of Ecology, School of Biology, Aristotle University of Thessaloniki, 54124 Thessaloniki, Greece* **2** *Department of Environmental and Natural Resources Management, G. Seferi 2, 30100, University of Ioannina, Agrinio, Greece* **3** *Environmental Conservation and Management Programme, School of Pure and Applied Sciences, Open University of Cyprus*

Corresponding author: *Nefta-Eleftheria Votsi* (nvotsi@bio.auth.gr)

Academic editor: *Douglas Evans* | Received 14 September 2011 | Accepted 31 January 2012 | Published 14 March 2012

Citation: Votsi N-E, Mazaris AD, Kallimanis AS, Zomeni MS, Vogiatzakis IN, Sgardelis SP, Pantis JD (2012) Road effects on habitat richness of the Greek Natura 2000 network. Nature Conservation 1: 53–71. doi: 10.3897/natureconservation.1.2086

Abstract

The road network has both positive and negative ecological effects, and understanding these helps identify environmentally preferable solutions for transportation policy and planning. We investigated the relationship between road density and habitat type richness of Greek protected areas. We used digital vector maps of 214 sites included in the Greek Natura 2000 network. We calculated road density for the terrestrial part of each site and correlated it with habitat type richness. Average road density of protected areas (0.377 km/km^2) was significantly lower than the national road density of Greece (0.446 km/km^2). We identified 32 sites that were not intersected by roads. These roadless sites were located at mountain tops, at islets, or in remote coastal zones. Overall we found no significant correlation between road density and habitat type richness. We suggest that the effect of road networks on habitat type richness is less apparent at landscapes with long history of human presence, because the landscape (and its habitat diversity) has coevolved with human activities over the past millennia. Our analysis provides a step towards quantifying the effect of road density on the diversity of habitats and consequently on species of conservation interest in international networks of protected areas such as the European Natura 2000 network.

Keywords

Habitat diversity, Natura 2000 network, Protected areas, Road ecology, Road network, Roadless areas, Greece

Introduction

Biodiversity loss has settled to one of the major environmental problems of the twenty first century, consequently countries worldwide have proceeded to establish protected areas in order to halt the loss and preserve species and habitats of high conservation value. In the European Union, the Natura 2000 network is the largest network for nature conservation extending to all member states. However despite the effort so far, the biodiversity crisis in Europe continues to deepen (EU 2010). Human activities, like habitat destruction and pollution, are considered a compelling driver of biodiversity loss (Salafsky et al. 2008). In particular, one of the major human activities affecting biodiversity in protected areas is transportation (Forman and Alexander 1998; Sherwood et al. 2003).

Roads have been reported to have both positive and negative effects on society, whilst reports on the negative impacts on ecological impacts have been widespread. Roads function as ecological corridors for dispersal for many species, but this implies the inclusion of alien and invasive species (Zhu et al. 2006). On the other hand, roadsides in intensive agricultural landscapes have a positive effect by maintaining native grassland plants and nesting sites for wildlife (Forman 2000). In urban landscapes roads function as a major driver for socio-economic changes (Zhu et al. 2006). Less recognized is the ecological protection resulting from 'bundling traffic' i.e. the concentration of traffic on main roads permitting the surrounding environment to be undisturbed. Nevertheless, recent studies indicate that the design of new road systems should take into account the bundling of roads instead of the uniform distribution across the landscape (Selva et al. 2011).

Among the negative road impacts are situations of altered animal behaviour due to roads (reviewed in Trombulak and Frissell 2000), landscape impermeability to small (Richardson et al. 1997; Gerlach and Musolf 2000) and larger mammals (Hansen 1983; Thiel 1985; McLellan and Shackleton 1988; Romin and Bissonette 1996) and increased amphibian mortality (Fahrig et al. 1995; Carr and Fahrig 2001, Cushman 2006). Physical and chemical conditions in areas subjected to road construction are altered (Trombulak and Frissell 2000) as are the hydrologic and geomorphologic attributes of a site (Jones et al. 2000). Moreover, vehicle collisions and increased human access to natural areas and reserves contribute to the decline of many species' populations (Benn and Herrero 2002; Kaczensky et al. 2004; Eigenbrod et al. 2008).

The majority of studies on biodiversity loss due to road networks emphasize the effects on species movement (e.g. Merriam et al. 1989; Vos and Chardon 1998), increased mortality (Rosen and Lowe 1994; Fahrig et al. 1995; Barthelmess and Brooks 2010), habitat fragmentation and edge effects (Mader 1984; Andrews 1990; Soulé et al. 1992; Thiollay 1993' Henjum et al. 1994; Wigley and Roberts 1994; Jaeger et al. 2007; Roedenbeck et al. 2007; Spellerberg 1998), invasion by exotic species (Lonsdale and Lane 1994), or increased human access to wildlife habitats (Graham et al. 2010), all of which are expected to increase local extinction rates or decrease local recolonization rates.

Compared to other land use alterations, roads may be the leading mechanism of fragmentation and habitat reduction in protected areas (Alkemade et al. 2009; Benítez-Lòpez et al. 2010). In addition, many studies have emphasized the effects of roads on fragmenting wildlife populations (Riley 2006; Strasburg 2006).

Over the past two decades an increased interest in the importance of roadless areas in biological conservation has been observed (DeVelice and Martin 2001; Selva et al. 2011). Although there has been a recent attempt in Europe to address roadless and low-traffic areas as conservation targets (Selva et al. 2011), most of research on the topic originates in the US and Australia (e.g. Strittholt and Dellasala 2001; Gelbard and Harrison 2003; Watts et al. 2007; Chen and Roberts 2008). In the US roadless areas play an important role in the conservation of biodiversity due to their size and location, but also to the adoption of the Roadless Rule environmental impact statement of the Forest Service (Crist et al. 2005). In Australia, on the other hand, nature conservation authorities have developed techniques for wilderness identification and analysis to assess the impact of roadless areas in management strategies (Lesslie 1991). In other parts of the word with longer history of human activity, as in Greece, roads mostly follow the tracks of ancient pathways, and several roads are known to have been in operation since ancient times (Faloso 2003). For the assessment of the road system in the Natura 2000 network, in this study, roadless areas denote protected sites not intersected by roads.

There is pressing need for protected areas' management to take into account road networks, since the ecological influences of roads may extend hundreds—or thousands—of meters from the roadside, suggesting a direct ecological road effect on most protected areas (Forman and Alexander 1998). The increase of protected areas in Europe following the implementation of the EU Habitats Directive (92/43/EEC) and in particular the Natura 2000 network (Council of European Communities 1992) saw an increase of roaded protected areas, which however has not been ensued by a corresponding increase of research regarding road effects on biodiversity (Colchester 1994; Apostolopoulou and Pantis 2009). Therefore, it is of utmost importance that the European Union includes roadless areas in its conservation policies (Selva et al. 2011). The Mediterranean basin is one of the world's biodiversity 'hotspots' containing a great variety of plant and animal taxa (Gaston and David 1994; Médail and Quézel 1999). In Greece, a country rich in biodiversity, the most important and actively managed protected areas prior to the designation of Natura 2000 network were National Parks, found mainly in mountainous areas with limited road network and human presence. However, with the implementation of Natura 2000 network many sites now include roads or are located in close proximity to intensively farmed land and coastal areas with tourist development (Papageorgiou and Vogiatzakis 2006). As a result, the majority of Natura 2000 sites in the country are inhabited and dissected by roads of variable traffic load.

Our goal was the interpretation of road effects on the ecology of protected areas in Greece, thus we focused on the effects of road density on habitat richness in Natura 2000 network. Since the study covers the entire country we considered a landscape level approach (Forman 2000; Forman and Deblinger 2000), which reflects landscape pattern analysis in relation to habitat suitability and ecological assessment (Riitters et al. 1996). The main objectives of this study were: a) to investigate which landscape characteristics (e.g. ecosystem type, altitude) influence road density in the protected sites and b) to examine if habitat richness within the Natura 2000 network is affected by road density.

Methods

Study area

Greece occupies an area of 131,990 km^2 and has a population of approximately 11 million. Nearly one third of the land comprises lowland plains, valleys and foothill country that is generally fertile and productive. The remaining two-thirds are mostly mountainous terrain. Variation of climatic conditions and geomorphologic characteristics as well as its geographic position create an impressive variety of vegetation types and habitats. In these habitats breed a diversity of terrestrial species (60% of which nest in Greece), reptiles, amphibians and freshwater fish (HZS 1992). Greece has also a rich flora, according to Dimopoulos et al. (pers. comm. 2012: Checklist of the Vascular Plants of Greece, currently in progress) which consists of c. 7000 vascular taxa (indigenous and naturalized aliens), while according to Strid and Tan (1997, 2002), Tan and Iatrou (2001), the estimated number of native plant taxa is 6437 or c. 5800 species. The plant diversity of Greece rates among the highest in Europe and the Mediterranean and includes 913 endemic species (Georghiou and Delipetrou 2010).

Greece, as a member state of the European Union, designated a national network of protected areas to be included in the European Natura 2000 network and by 2011 a total of 419 sites was included in the Greek Natura 2000 database. The study area includes the entire Natura 2000 network in Greece, after taking into account the overlaps of sites designated under the Birds (SPAs) and those under the Habitats (SCIs) Directives, which includes 371 sites and covers more than 22% (29,249 km^2) of the national terrestrial area. These sites cover most geological formations present in Greece (Higgins and Higgins 1996) and range in elevation from 0 to 2,917 m.

Datasets

We studied 214 terrestrial sites included in the Greek Natura 2000 network, for which digital habitat maps were available (60.45% of Natura 2000 terrestrial sites). For these sites the total terrestrial area was calculated after omitting any aquatic (marine or freshwater) areas. A map of the road system (1:500,000 scale) was overlaid on the Natura 2000 network and GIS analyses were performed using ArcGIS software (ESRI 2005).

The road map included all tarmac roads (high quality carriageways, dual carriageways, regional and local roads). Information on forest roads was not available and therefore not included in the analysis. We calculated road density for all sites and had access to similar data for the country as a whole. Based on the Natura 2000 database, we derived information regarding the number of habitat types in the 214 selected sites. In total, 101 different habitat types were recognised. The habitat type richness in our case corresponds to habitats listed on Annex I of the Habitats Directive (92/43/EEC) which identifies habitat types as aspects of biodiversity for which SCI have to be proposed to be monitored (Dimopoulos et al. 2006; Evans 2006; Drakou et al. 2011). It is acknowledged that the habitat type affects ecosystem function, and thus it could be considered as an indicator of biodiversity (Thies and Tscharntke 1999). Finally, a topographic map of Greece (scale 1: 100000) was also used in order to assess the altitudinal distribution of Natura 2000 sites in relation to road density.

Data analysis

The 214 sites of the Natura 2000 network were characterised as either coastal, forest or freshwater based on the dominant land use and habitat types according to the EU Habitats Directive (92/43/EEC). This information was derived from the Natura 2000 and CORINE Land Cover databases.

We also employed Vector-based Landscape Analysis Tools (version 1.1, Lang and Tiede 2003) to calculate three major fragmentation indices namely landscape division, splitting index, effective mesh size as well as the number of patches due to roads for each Natura 2000 site. Landscape division, splitting index and effective mesh size are three quantitative measures that characterize landscape fragmentation in a geometric perspective (Jaeger 2000). Explanatory information regarding fragmentation metrics is shown in Appendix.

To investigate for any potential relationship between road density across Natura 2000 sites and fragmentation metrics we used non parametric Spearman correlation coefficient; the analysis was repeated by grouping sites within each ecosystem type (i.e. coastal, forest, freshwater). We further used Kruskal-Wallis test to investigate the potential differences between the fragmentation metrics in the three ecosystem types. The relationship between road density and the surface of the sites was assessed by means of linear regression.

Mixed-model regression was applied to analyse the relationship between the road density (dependent variable), habitat richness and altitude (covariates) and their interactions. Ecosystem category was entered as a random factor.

Variables were transformed (log or square root) as necessary to meet assumptions of normality and homoscedasticity of residuals.

A linear regression was applied to provide a more thorough investigation of the relationship between road density and habitat richness.

All statistical analyses were performed with SPSS 18.0 (SPSS 2009).

Results

The total length of roads in the Natura 2000 network is 8,625 km while the total surface of Natura 2000 sites intersected by roads is 23,199 km^2. Average road density for the whole 214 sites was 0.37 km/km^2 (Fig. 1). 32 sites were found to be roadless, 17 of which are coastal, 9 are forest and 6 are freshwater ecosystems. The total area of roadless sites ranged from 1.29 to 109.33 km^2 (mean: 26.87 ± 29.01 km^2), which was significantly smaller compared to the remaining 182 roaded sites of the network (mean: 127.46 ± 151.87 km^2) ($P<0.01$). The mean altitude of roadless areas was 257.51 m (± 464.67 m) while the mean altitude of roaded sites was 566.26 m (± 522.90).

Road density in these sites ranged from 0.0004 km/km^2 to 2.46 km/km^2. The mean road density of the protected areas was significantly lower than the national road density (0.44 km/km^2) (all sites: $P<0.01$; roaded sites: $P<0.01$). The distribution of road density values in studied sites (n=214) was right skewed; half the areas had low road densities (less than 0.3 km/km^2) and only three had road densities greater than 1.50 km/km^2 (Fig. 2). Most roaded sites (97%) were intersected by regional roads and/or local roads (76%) and less than half of the protected areas (46%) were crossed by dual carriageways. Roaded sites within the Natura 2000 network

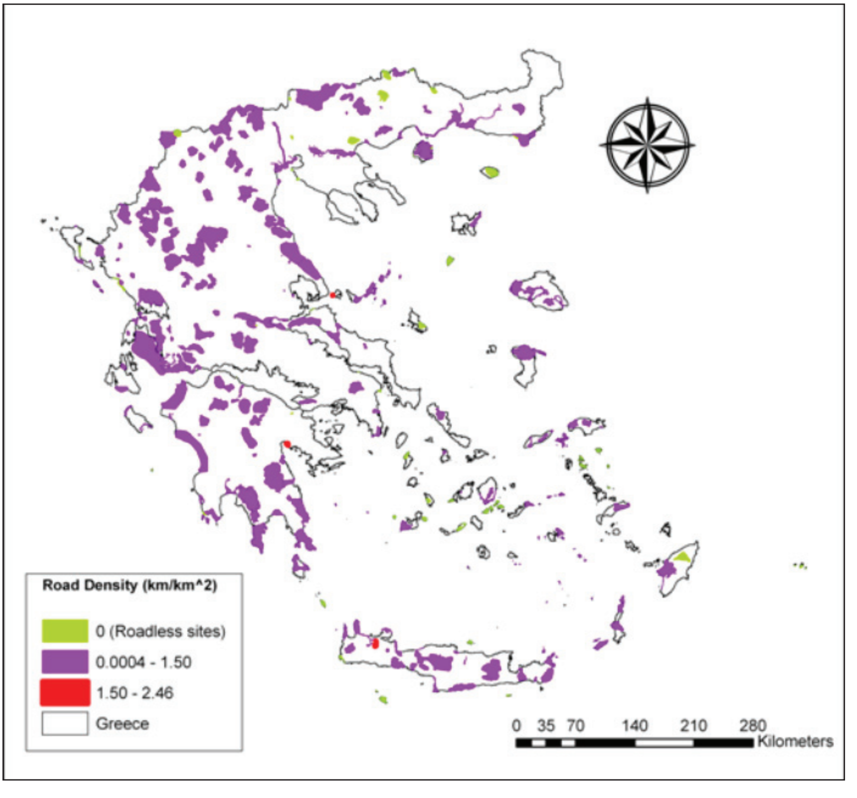

Figure 1. Road density at the Greek Natura 2000 network. Road density values (km/km^2) for each one of the 214 studied sites of the Natura 2000 network in Greece. Values ranging from 0 to 2.46 km/km^2.

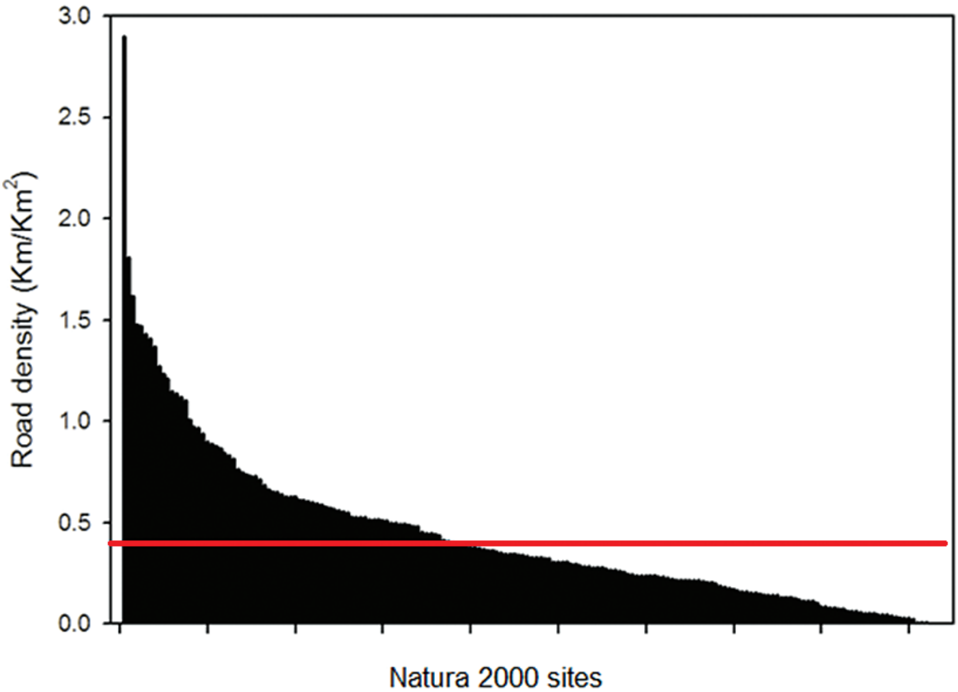

Figure 2. Distribution of road density at Greek Natura 2000 sites. The distribution of road density values (km/km^2) in descending order at the 214 studied sites of the Greek Natura 2000 network. The red line depicts the overall national road density, including Natura 2000 sites.

demonstrated a significant lower mean density of local (mean= 0.23±0.32 km/km^2) and regional (mean= 0.09±0.14 km/km^2) roads compared to the country as a whole (in both cases P<0.01). Road density of forested and coastal sites was significantly lower than the national average road density (P<0.01). In contrast, we found no significant difference between road density in freshwater aquatic sites and national road density (P=0.46).

We found no significant correlation between a site's surface area and road density (P = 0.09).

Our analysis revealed positive and significant correlations between road density and landscape division (r_s= 0.59, P<0.01), splitting index (r_s= 0.58, P<0.01) and number of patches (r_s= 0.46, P<0.01). Similar results were obtained when repeating the analysis by grouping protected sites as coastal, forest and freshwater ecosystems. In contrast, road density was negatively correlated with effective mesh size (r_s= -0.17, P<0.05); which however, was not significantly associated with road density when grouping our data into the three ecosystem types.

Effective mesh size was significantly different among the three ecosystem types (Kruskal-Wallis test H=11.29, P<0.01) with higher values supported at the forested sites. No other significant difference was indicated for the fragmentation metrics among the studied ecosystems types (in all cases P>0.05) (Table 1).

Table 1. Descriptive landscape characteristics of road fragmentation in Natura 2000 network based on the three ecosystem types.

Ecosystem Type	mean Landscape division	mean Splitting index	mean Effective mesh size (km^2)	mean Number of pathes	mean Surface area (km^2)	mean Habitat types/ site	mean Road density (km/km^2)	mean Altitude (m)
coastal	34.32 (± 29.18)	2.09 (± 1.51)	45.29 (± 105.23)	12.25 (± 13.08)	84.33 (± 148.29)	11.6	0.36 (± 0.42)	131.67 (± 156.66)
forest	28.15 (± 25.83)	1.65 (± 0.78)	102.77 (± 94.02)	13.90 (± 14.47)	154.88 (± 137.42)	8.47	0.29 (± 0.29)	971.50 (± 468.42)
freshwater	34.86 (± 27.06)	1.94 (± 1.14)	44.4 (± 61.65)	15.27 (± 21.56)	84.55 (± 139.78)	9.8	0.49 (± 0.30)	309.8 (± 378.58)

When the mixed-model regression was implemented road density was not related to either habitat richness (P=0.29), mean site altitude (P=0.32) or their interaction (P=0.73). Road density was found to be related to ecosystem type (P<0.05) with a higher value observed at freshwater ecosystems (mean=0.49 km/km^2) than in coastal (mean=0.36 km/km^2) and forests (mean=0.29 km/km^2).

In Figure 3 the relationship between habitat richness and road density is illustrated. Sites with low road density values could support either low or high habitat

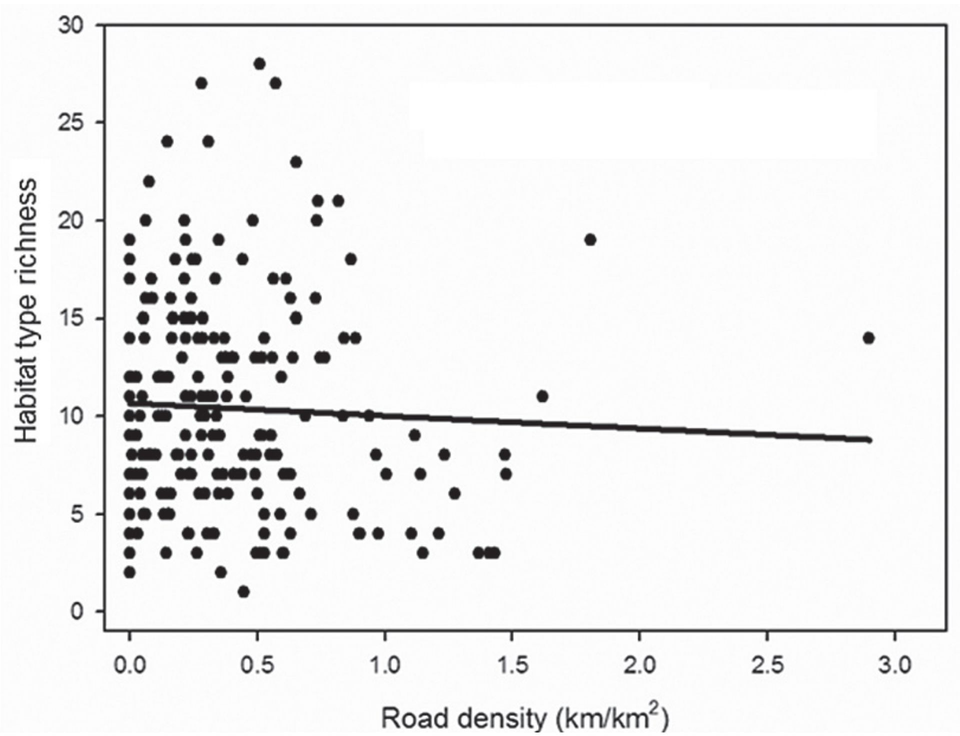

Figure 3. Road density in relation to habitat richness. The relationship of road density (untransformed values) with habitat type richness for the 214 studied sites of the Greek Natura 2000 network.

diversity. But as road density increases the variance in habitat richness values among sites decreases. At high road density values, medium habitat richness was observed. Finally, we did not identify any significant correlation between road density and habitat diversity within any of the three ecosystem types.

Discussion

Although Europe is considered to be the most highly fragmented continent (Selva et al. 2011), the majority of ecological research on the effects of roads and the importance of roadless areas for conservation biology comes mainly from the US. Greece shows an overall low average road density (0.44 km/km^2) compared to the US (1.2 km/km^2) (Forman 2000). Even greater divergence is shown when comparing Greece to the Netherlands (3 km/km^2) (EEA 2002). These differences are even more striking considering the greater population density in Greece (85.3 persons/km^2) in comparison to the US (31 persons/km^2). Such differences in road density (Forman and Alexander 1998, Spellerberg 1998) are likely to reflect national policies (Apostolopoulou and Pantis 2009), urbanization, development and infrastructure (Georgi and Dimitriou 2010) but are probably also influenced by topographic factors as well as different historic paths in road planning and construction. Especially in Greece, roads mostly follow the tracks of ancient pathways, and several roads are known to have been in operation since ancient times (Faloso 2003). The range of road density values observed in protected areas in Greece is comparable to that of the northern Great Lakes Region in North America (Saunders et al. 2002) and the native forest ecosystems of the US, which also include protected areas (Heilman et al. 2002). On the other hand, the high road density values (>1.5 km/km^2) found in certain Greek Natura 2000 sites are comparable to those of densely populated countries such as the US (Forman and Alexander 1998), which is surprising considering their high conservation value. For instance, Olympia the original home of the Olympic Games is a Natura 2000 site (sitecode GR 2330004) with high road density (1.43 km/km^2).

Considering the conservation value of roadless areas and the sparse road network in Greece, one might intuitively expect that the majority or at least a high proportion of Greek protected areas would be roadless. Surprisingly though, protected areas without roads represent 15% of the studied sites, covering less than 3% of the area protected under the Greek Natura 2000 network. Nevertheless, these 32 roadless sites might play a significant role in future conservation efforts (Selva et al. 2011).Many roadless protected sites are in mountainous areas. Although topography does not favour road construction in mountains, nevertheless this could be an artefact since no data on forest roads was available. There are also numerous coastal roadless areas which actually represent rocky islets or remote and possibly inaccessible coastal zones. Similarly, roadless wetlands are either of limited accessibility (located alongside a freshwater aquatic ecosystem subjected to seasonal rises in water level) or cannot be accessed at all (sites with riparian ecosystems whose deltas are large areas covered by sediment).

Our results regarding the representation of roadless areas at different elevation ranges are in agreement with similar work in the US, where in many cases roadless areas occur at lower to mid-elevations (DeVelice and Martin 2001; Strittholt and Dellasala 2001) as well as at mid to higher elevations (Crist et al. 2005). Similarly, road density in roaded sites showed no significant difference with altitude. The lack of correlation suggests that a combination of topographic features and anthropogenic factors influence the development of road networks, leading to complicated patterns (Turner 1989). However, human needs chiefly dictate road construction in Greece whilst topography or landscape characteristics are of less importance (Tzatzanis et al. 2003).

Several studies on road effects have used road density as an indicator for species presence or persistence and they have reported a significant range of critical values for different species (Van Dyke et al. 1986; Mech 1989; Minor and Urban 2010). However, in the present study we focus on habitat type richness, not species presence. In reality, critical values could vary among landscapes depending on the scale of analysis, differences in history and evolution. Landscapes with long history of human presence, as in our case study, have coevolved with humans and currently support complex compositional and structural components of ecological biodiversity making the effects of roads less apparent (Angelstam 1997). Almost all Greek landscapes have been shaped, to a certain extent, by human activities, and semi-natural landscapes are often recognized as highly diverse areas (Papanastasis et al. 2011). In fact, part of the Greek road network, which intersects a large number of Natura 2000 sites, is known to have been in operation since antiquity (Dinsmoor 1975). Biodiversity conservation at the ecosystem level is advocated as a means to sustain both ecological processes and the species present (e.g. Noss and Cooperrider 1994). Therefore, we have focused on habitat types which include vegetation structure, biodiversity and ecosystem functions. Moreover, the Natura 2000 network was established explicitly for the preservation of natural and semi-natural habitats (see Habitats Directive 92/43/EEC). A better understanding of the effects of roads on habitat richness would result from an investigation of the habitat types in relation to non protected areas. However, such data is not available for Greece.

A closer analysis for the sites with dense road network (>1.5 km/km^2) revealed that their high road density values are mainly attributed to their spatial characteristics (extent, shape) and intense human activity. These three sites are of relatively limited extent (0.4 to 4.96 km^2) and have an elongated shape. One of these sites is a canyon, with elongated shape and small area (4.96 km^2). The other two sites are located in the coastal zones of two highly populated islands popular with tourists. In these latter cases, the intense and permanent human activity in the area has resulted in a dense road system, without apparently affecting the area's ability to support a rich biodiversity. Nine out of the thirteen sites with road densities greater than 1km/km^2 are areas where no conservation status was assigned prior to their incorporation in the Natura 2000 network. This might imply that natural areas which host important habitat types but are not protected under national or European legislation, have been vulnerable to the expansion of the road network in Greece.

Fragmentation metrics are advocated as a powerful tool for the quantification of landscape patterns (Corry and Nassauer 2005). Landscape division, splitting index effective mesh size and number of patches depict the process in a geometric perspective and they respond well to dissection as caused by roads (Jaeger 2000). Road density showed a strong relationship with all fragmentation metrics. Landscape division, splitting index and number of patches constitute patch-based indicators, which actually describe the degree of fragmentation in a landscape (Schneider and Woodcock 2008). These are found positively correlated in our study area indicating landscape's degradation in terms of ecological processes (Millington et al. 2003). In contrast, as road density increases, effective mesh size decreases; this also emerges landscape's degradation due to fragmentation (Girvetz et al. 2008). Fragmentation metrics were differentiated in the case of effective mesh size as far as the ecosystem types are concerned. As already mentioned by Jaeger (2000), effective mesh size is an expression of the probability that two places in the landscape can be connected. In our case, it seems that forest sites constitute a separate category, with unfragmented areas, while freshwater and coastal ecosystem types follow a similar pattern, with a higher degree of degradation due to fragmentation. To sum up, our findings regarding road fragmentation come in accordance to relevant previous studies (Heilman et al. 2002; Li et al. 2004) highlighting however, the diverging pattern of road fragmentation in forest ecosystem types.

As far as the ecosystem types are concerned, we found that road density is associated with specific land use types. The classification of the 214 Natura 2000 sites in three basic ecosystem types was based on the prevailing habitat type (according to Annex I of the Natura 2000 database) in relation to the main land use type (according to CORINE Land Cover database) of each site. There are many cases where habitats present in a site might not be listed in Annex I. Thus we also used CORINE Land Cover database in order to identify the dominant ecosystem type in each site. Freshwater sites showed higher road density values compared to forest sites. Freshwater sites in Greece are frequently under human pressure since they share borders with fertile agricultural lands (Drakou et al. 2008, Kallimanis et al. 2008a). Extensive cultivated fields require a dense network of roads, for both the access of heavy agricultural machinery and the transport of agricultural goods. Similarly, they indicate the existence of economically active local communities, thereby a high associated need for transportation and road infrastructure (Hawbaker and Radeloff 2004). Intense human activity in many areas in Greece has resulted in dense road systems in certain sites included in the Natura 2000 network, without however an apparent effect on the areas' ability to support a rich biodiversity, since road density is not significantly correlated to habitat richness. Despite the dense road network, the continuous human presence, lack of protection status and absence of management measures, the studied sites support numerous habitat types of conservation interest.

According to our findings, a correlation between road density and habitat richness is lacking, which comes to contradict other studies (Andrews 1990; Noss and Cooperrider 1994; Trombulak and Frissell 2000). Nevertheless, in these cases countries with high road densities were examined, while, in our study Greece demonstrates a low road density possibly explaining the absence of correlation. Alternatively, the choice of temporal and spatial scale for analysis might have influenced the patterns observed. Many authors have stressed the importance of identifying the right scale in time and/or space for ecological monitoring and impact assessment (Underwood 1994; Findlay and Zheng 1997). Findlay and Bourdages (2000) stress that there is usually a lag between road construction and ecosystem response, therefore considering the time dimension is essential when studying the effects of roads. Information on changes in habitat richness over time would allow a more detailed evaluation of possible road effects. However, such information was not available. In addition, we suggest that information regarding habitat richness in areas outside of the Natura 2000 network, might have also been valuable regarding the nature of the identified spatial patterns, therefore, similar studies should provide such analyses if this type of information is available.

Another facet of consideration is the component of biological diversity that we chose to study (i.e. genetic, species, ecosystem, landscape level) (CEQ 1993). Whilst previous work has shown that richness of a particular taxon may react immediately to anthropogenic changes (e.g. Karr et al. 1987), responses to the effects of road construction on a higher level such as species richness may not be immediately apparent (Findlay and Bourdages 2000). We know that habitat richness in these sites affects species richness (Kallimanis et al. 2008b); however, this does not necessarily mean that road effects are not manifested at the species level.

Our focal area of interest in this paper has been habitat diversity, so we did not analyze habitat fragmentation, which in other cases has proven an important effect of the road network (Jaeger et al. 2007). Finally, due to the lack of data we were not able to investigate the effects of traffic volume and speed, which often are of influence (Eigenbrod et al. 2008). Perhaps road density *per se* is not a sufficient measure of the impacts of roads; traffic load information might have resulted in different findings (Van Langevelde and Jaarsma 2004). This remains an open research question for future work.

Conclusions

Overall and despite the possible adverse effects of roads on species, we found that in Greek protected natural areas road density was not correlated to a site's habitat richness. This might indicate that currently the road density of Greek Natura 2000 areas is below a critical level and thus any adverse effects are not apparent. Alternatively, this could suggest that the long history of human presence might have ameliorated the adverse effects and through co-evolution a new semi-natural landscape of high diversity has been established.

Acknowledgments

The work was supported by the EU FP7 SCALES project ("Securing the Conservation of biodiversity across Administrative Levels and spatial, temporal and Ecological Scales"; project #226852). We would like to thank two anonymous reviewers for their comments on an earlier version of the manuscript.

References

Alkemade R, van Oorschot M, Miles L, Nellemann C, Bakkenes M, ten Brink B (2009) GLOBIO3: a framework to investigate options for reducing global terrestrial biodiversity loss. Ecosystems 12: 374–390. doi: 10.1007/s10021-009-9229-5

Andrews A (1990) Fragmentation of habitat by roads and utility corridors: a review. Australian journal of Zoology 26: 130–141.

Angelstam P (1997) Landscape analysis as a tool for the scientific management of biodiversity. Ecological Bulletins 46: 140–170.

Apostolopoulou E, Pantis JD (2009) Conceptual gaps in the national strategy for the implementation of the European Natura 2000 conservation policy in Greece. Biological Conservation 142: 221–237. doi: 10.1016/j.biocon.2008.10.021

Barthelmess EL, Brooks MS (2010) The influence of body-size and diet on road-kill trends in mammals. Biodiversity and Conservation 19: 1611–1629. doi: 10.1007/s10531-010-9791-3

Benítez-Lȯpez A, Alkemade R, Verweij PA (2010) The impacts of roads and other infrastructure on mammal and bird populations: a meta-analysis. Biological Conservation 143: 1307–1316.

Benn B, Herrero S (2002) Grizzly bear mortality and human access in Banff and Yoho National Parks, 1971–98. Ursus 13: 213–221.

Carr LW, Fahrig L (2001) Effect of road traffic on two amphibian species of differing vagility. Conservation Biology 15: 1071–1078. doi: 10.1046/j.1523-1739.2001.0150041071.x

Chen X, Roberts KA (2008) Roadless areas and Biodiversity: a case study in Alabama, USA. Biodiversity and Conservation 17: 2013–2022. doi: 10.1007/s10531-008-9351-2

Council on Environmental Quality (1993) Incorporating biodiversity considerations into environmental impact analysis under the national environmental policy act. Washington, DC, US Government Printing Office.

Colchester M (1994) Salvaging nature. Indigenous peoples, protected areas and biodiversity conservation. United Nations Research Institute for Social Development (UNRISD), World Rainforest movement, World Wide Fund for Nature.

Corry RC, Nassauer JI (2005) Limitations of using landscape pattern indices to evaluate the ecological consequences of alternative plans and designs. Landscape Urban Planning 72: 265–280. doi: 10.1016/j.landurbplan.2004.04.003

Council of European Communities (1992) Council Directive 92/43 EEC of 21 May 1992 on the Conservation of Natural Habitats and Wild Fauna and Flora. Official Journal of

European Communities No. L206/7. http://eur-lex.europa.eu/LexUriServ/LexUriServ.do?uri=CELEX:01992L0043-20070101:EN:NOT

Crist MR, Wilmer B, Aplet GH (2005) Assessing the value of roadless areas in a conservation reserve strategy: biodiversity and landscape connectivity in the northern Rockies. Journal of Applied Ecology 42: 181–191. doi: 10.1111/j.1365-2664.2005.00996.x

Cushman SA (2006) Effects of habitat loss and fragmentation on amphibians: A review and prospectus. Biological Conservation 128: 231–240. doi: 10.1016/j.biocon.2005.09.031

DeVelice RL, Martin JR (2001) Assessing the extent to which roadless areas complement the conservation of biological diversity. Ecological Applications 11: 1008–1018. doi: 10.1890/1051-0761(2001)011[1008:ATETWR]2.0.CO;2

Dimopoulos P, Bergmeier E, Fischer P (2006) Natura 2000 Habitat Types of Greece Evaluated in the Light of Distribution, threat and Responsibility. Biology and Environment: Proceedings of the Royal Irish Academy 106: 175–187. doi: 10.3318/BIOE.2006.106.3.175

Dinsmoor WB (1975) The architecture of ancient Greece: an account of its historic development. Batsford, London, 426 pp.

Drakou EG, Kallimanis AS, Sgardelis SP, Pantis JD (2008) Landscape structure and habitat composition in reservoirs, lakes, and rivers. Lake and Reservoir Management 24: 244–260. doi: 10.1080/07438140809354065

Drakou EG, Kallimanis AS, Mazaris AD, Apostolopoulou E, Pantis JD (2011) Habitat type richness associations with environmental variables: a case study in the Greek Natura 2000 aquatic ecosystems. Biodiversity and Conservation 20: 929–943. doi: 10.1007/s10531-011-0005-4

ESRI (2005) ArcView 3.2 Software. Environmental Systems Research Institute, Redlands, CA.

European Union (2010) Biodiversity: Assessment confirms EU has missed 2010 target, but important lessons learned IP/10/1303. http://europa.eu/rapid/pressReleasesAction.do?reference=IP/10/1303&type=HTML

Eigenbrod F, Hecnar SJ, Fahrig L (2008) The relative effects of road traffic and forest cover on anuran populations. Biological Conservation 141: 35–46. doi: 10.1016/j.biocon.2007.08.025

Evans D (2006) The Habitats of the European Union Habitats Directive. Biology and Environment: Proceedings of the Royal Irish Academy 106: 167–173. doi: 10.3318/BIOE.2006.106.3.167

Fahrig L, Pedlar JH, Pope SE, Taylor PD, Wegner JF (1995) Effect of road traffic on amphibian density. Biological Conservation 73: 177–182. doi: 10.1016/0006-3207(94)00102-V

Faloso M (2003) La via Egnatia, Vol.1, Da Appolonia Dyrrachium ad Herakleia Lynkestdos, Instituto Grafico Editoriale Romano, Rome.

Findlay CS, Bourdages Z (2000) Response time of wetland biodiversity to road construction on adjacent lands. Conservation Biology 14: 86–94. doi: 10.1046/j.1523-1739.2000.99086.x

Findlay CS, Zheng L (1997) Determining characteristic stressor scales for ecosystem monitoring and assessment. Journal of Environmental Management 50: 265–282. doi: 10.1006/jema.1996.0109

Forman RTT (2000) Estimate of the area affected ecologically by the road system in the United States. Conservation Biology 14: 31–35. doi: 10.1046/j.1523-1739.2000.99299.x

Forman RTT, Alexander LE (1998) Roads and their major ecological effects. Annual Review of Ecology and Systematics 29: 207–231. doi: 10.1146/annurev.ecolsys.29.1.207

Forman RTT, Deblinger RD (2000) The ecological road-effect zone of a Massachusetts (U.S.A.) suburban highway. Conservation Biology 14: 36–46. doi: 10.1046/j.1523-1739.2000.99088.x

Gaston KJ, David R (1994) Hotspots across Europe. Biodiversity Letters 2: 108–116. doi: 10.2307/2999714

Gerlach G, Musolf K (2000) Fragmentation of landscape as a cause for genetic subdivision in bank voles. Conservation Biology 14: 1066–1074. doi: 10.1046/j.1523-1739.2000.98519.x

Georgi JN, Dimitriou D (2010) The contribution of urban green spaces to the improvement of environment in cities: case study of Chania, Greece. Building and Environment 45: 1401–1414. doi: 10.1016/j.buildenv.2009.12.003

Graham K, Boulanger J, Duval J, Stenhouse G (2010) Spatial and temporal use of roads by grizzly bears in west-central Alberta. Ursus 21: 43–56. doi: 10.2192/09GR010.1

Gelbard JL, Harrison S (2003) Roadless habitats as refuges for native grasslands: interactions with soil, aspect, and grazing. Ecological Applications 13: 404–415. doi: 10.1890/1051-0761(2003)013[0404:RHARFN]2.0.CO;2

Georghiou K, Delipetrou P (2010) Patterns and traits of the endemic plants of Greece. Botanical Journal of the Linnean Society 162, 130–422. doi: 10.1111/j.1095-8339.2010.01025.x

Girvetz EH, Thorne JH, Berry AM, Jaeger JAG (2008) Integration of landscape fragmentation analysis into regional planning: a statewide multi-scale case study from California. Landscape and Urban Planning 86: 205–218. doi: 10.1016/j.landurbplan.2008.02.007

Hansen CS (1983) Costs of deer-vehicle accidents in Michigan. Wildlife Society Bulletin 11: 161–164.

Hawbaker TJ, Radeloff VC (2004) Roads and landscape pattern in northern Wisconsin based on a comparison of four road data sources. Conservation Biology 18: 1233–1244. doi: 10.1111/j.1523-1739.2004.00231.x

Heilman GEJR, Strittholt JR, Slosser NC, Dellasala DA (2002) Forest fragmentation of the conterminous United States: Assessing forest intactness through road density and spatial characteristics. Bioscience 52: 411–422. doi: 10.1641/0006-3568(2002)052[0411:FFOTCU]2.0.CO;2

Henjum MG, Karr JR, Bottom DL, Wright S, Bednarz J, Perry D, Beckwitt S, Karr JR (1994) Interim protection for late-successional forests, fisheries and watersheds, national forests east of the Cascade crest, Oregon and Washington. The Wildlife Society. Bethesda, MD, 245 pp.

Higgins MD, Higgins RA (1996) A Geological companion to Greece and the Aegean. Cornell University Press, 240 pp.

Hellenic Zoological Society (1992) The Red Data Book of threatened vertebrates of Greece. Thymeli Publications, Athens, 356 pp.

Jaeger JAG (2000) Landscape division, splitting index and effective mesh size: new measures of landscape fragmentation. Landscape Ecology 15: 115–130. doi: 10.1023/A:1008129329289

Jaeger JAG, Schwarz-von Raumer H-G, Esswein H, Móller M, Schmidt-Lóttmann (2007) Time series of landscape fragmentation caused by transportation infrastructure and urban development: a case study from Baden-Wórttemberg, Ecology and Society 12: 22. http://www.ecologyandsociety.org/vol12/iss1/art22/

Jones JA, Swanson FJ, Wemple BC, Snyder KU (2000) Effects of roads on hydrology, geomorphology, and disturbance patches in stream networks. Conservation Biology 14: 76–85. doi: 10.1046/j.1523-1739.2000.99083.x

Kaczensky P, Blazic M, Gossow H (2004) Public attitudes towards brown bears (*Ursus arctos*) in Slovenia. Biological Conservation 118: 661–674. doi: 10.1016/j.biocon.2003.10.015

Kallimanis AS, Tsiafouli MA, Pantis JD, Mazaris AD, Matsinos Y, Sgardelis SP (2008a) Arable land and habitat diversity in Natura 2000 sites in Greece. Journal of Biological Research 9: 55–66.

Kallimanis AS, Mazaris AD, Tzanopoulos J, Halley JM, Pantis JD, Sgardelis SP (2008b) How does habitat diversity affect the species-area relationship? Global Ecology and Biogeography 17: 532–538. doi: 10.1111/j.1466-8238.2008.00393.x

Karr JR, Yant PR, Fausch KD (1987) Spatial and temporal variability of the index of biotic integrity in three Midwestern streams. Transactions of American Fisheries Society 116: 1–11. doi: 10.1577/1548-8659(1987)116<1:SATVOT>2.0.CO;2

Lang S, Tiede D (2003) vLATE Extension für ArcGIS – vektorbasiertes Tool zur quantitativen Landschaftsstrukturanalyse, ESRI Anwenderkonferenz 2003 Innsbruck. [CDROM]

Lesslie R (1991) Wilderness survey and evaluation in Australia. Australian Geography 22: 35–43. doi: 10.1080/00049189108703019

Li S, Xu Y, Zhou Q, Wang L (2004) Statistical Analysis on the Relationship between Road Network and Ecosystem Fragmentation in China. Progress in Geography 23: 77–85.

Lonsdale WM, Lane AM (1994) Tourist vehicles as vectors of weed seeds in Kakadu National Park, Northern Australia. Biological Conservation 69: 277–283. doi: 10.1016/0006-3207(94)90427-8

Mader HJ (1984) Animal habitat isolation by roads and agricultural fields. Biological Conservation 29: 81–96. doi: 10.1016/0006-3207(84)90015-6

McLellan BN, Shackleton DM (1988) Grizzly bears and resource-extraction industries: effects of roads on behaviour, habitat use and demography. Journal of Applied Ecology 25: 451–460. doi: 10.2307/2403836

Mech LD (1989) Wolf population survival in an area of high road density. American Midland Naturalist 121: 387–89. doi: 10.2307/2426043

Médail F, Quézel P (1999) Biodiversity Hotspots in the Mediterranean Basin: Setting Global Conservation Priorities. Conservation Biology 13: 1510–11513. doi: 10.1046/j.1523-1739.1999.98467.x

Merriam G, Kozakiewicz M, Tsuchiya E, Hawley K (1989) Barriers as boundaries for metapopulations and demes of *Peromyscus leucopus* in farm landscapes. Landscape Ecology 2: 227–235. doi: 10.1007/BF00125093

Millington AC, Velez-Liendo XM, Bradely AV (2003) Scale dependence in multitemporal mapping of forest fragmentation in Bolivia: implications for explaining temporal trends in landscape ecology and applications to biodiversity conservation. ISPRS Journal of photogrammetry and remote sensing 57: 289–299. doi: 10.1016/S0924-2716(02)00154-5

Minor E, Urban D (2010) Forest bird communities across a gradient of urban development. Urban Ecosystems 13: 51–71. doi: 10.1007/s11252-009-0103-1

Noss RF, Cooperrider AY (1994) Saving nature's legacy: protecting and restoring biodiversity. Defenders of Wildlife and Island Press, Washington, DC, 443 pp.

Papageorgiou K, Vogiatzakis IN (2006) Nature Protection in Greece: An appraisal of the factors shaping integrative conservation and policy effectiveness. Environmental Science and Policy 9: 476–486. doi: 10.1016/j.envsci.2006.03.003

Papanastasis PV, Arianoutsou M, Papanastasis K (2011) Environmental conservation in classical Greece. Journal of Biological Research-Thessaloniki 14: 123–135.

Richardson JH, Shore RF, Treweek JR, Larkin SBC (1997) Are major roads a barrier to small mammals? Journal of Zoology 243: 840–846. doi: 10.1111/j.1469-7998.1997.tb01982.x

Riley SPD (2006) Spatial Ecology of Bobcats and Gray Foxes in Urban and Rural Zones of a National Park. Journal of Wildlife Management 70: 1425–1435. doi: 10.2193/0022-541X(2006)70[1425:SEOBAG]2.0.CO;2

Riitters KH, O'Neill RV, Jones KB (1996) Assessing habitat suitability at multiple scales: a landscape-level approach. Biological Conservation 8: 191–202.

Roedenbeck IA, Fahrig L, Findlay CS, Houlahan JE, Jaeger JAG, Klar N, Kramer-Schadt S, van der Grift (2007) The Rauischholzhausen agenda for road ecology. Ecol Soc 12: 11. http://www.ecologyandsociety.org/vol12/iss1/art11/

Romin LA, Bissonette JA (1996) Deer-vehicle collisions: Status of state monitoring activities and mitigation efforts. Wildlife Society Bulletin 24: 276–283.

Rosen PC, Lowe CH (1994) Highway mortality of snakes in the Sonoran Desert of southern Arizona. Biological Conservation 68: 143–148. doi: 10.1016/0006-3207(94)90345-X

Salafsky N, Salzer D, Stattersfield AJ, Hilton-Taylor C, Neugarten R, Butchart SHM, Collen B, Cox N, Master LL, O'connor S, Wilkie D (2008) A standard lexicon for biodiversity conservation: Unified classifications of threats and actions. Conservation Biology 22: 897–911. doi: 10.1111/j.1523-1739.2008.00937.x

Saunders SC, Mislivets MR, Chen J, Cleland DT (2002) Effects of roads on landscape structure within nested ecological units of the Northern Great Lakes Region, USA. Biological Conservation 103: 209–225. doi: 10.1016/S0006-3207(01)00130-6

Selva N, Kreft S, Kati V, Schluck M, Jonsson BG, Mihok B, Okarma H, Ibisch PL (2011) Roadless and low-traffic areas as conservation targets in Europe. Environmental Management 48: 865–877. doi: 10.1007/s00267-011-9751-z

Sherwood B, Cutler DF, Burton JA (2003) Wildlife and roads: the ecological impact. Imperial College Press, 299 pp.

Schneider A, Woodcock CE (2008) Compact, Dispersed, Fragmented, Extensive? A Comparison of Urban Growth in Twenty-five Global Cities using Remotely Sensed Data, Pattern Metrics and Census Information. Urban Studies 45: 659–692. doi: 10.1177/0042098007087340

Soulé ME, Alberts AC, Bolger DT (1992) The effects of habitat fragmentation on chaparral plants and vertebrates. Oikos 63: 39–47. doi: 10.2307/3545514

Spellerberg IF (1998) Ecological effects of roads and traffic: a literature review. Global Ecology and Biogeography 7: 317–333. doi: 10.1046/j.1466-822x.1998.00308.x

SPSS (2009) SPSS 18.0 User's guide. SPSS, Chicago, Illinoise, USA.

Strasburg JL (2006) Conservation biology: Roads and genetic connectivity. Nature 440: 875–876. doi: 10.1038/440875a

Strid A, Tan K (1997) Flora hellenica 1. Königstein: Koeltz Scientific Books.

Strid A, Tan K (2002) Flora hellenica 2. Ruggell: Koeltz Scientific Books.

Strittholt JR, Dellasala DA (2001) Importance of roadless areas in biodiversity conservation in forested ecosystems: Case study of the Klamath-Siskiyou ecoregion of the United States. Conservation Biology 15: 1742–1754. doi: 10.1046/j.1523-1739.2001.99577.x

Tan K, Iatrou G (2001) Endemic plants of Greece, the Peloponnese. Gads Publishers Ltd, Copenhagen, 479 pp.

Thiel RP (1985) Relationship between road densities and wolf habitat suitability in Wisconsin. American Midland Naturalist 113: 404–407. doi: 10.2307/2425590

Thies C, Tscharntke T (1999) Landscape structure and biological control in agroecosystems. Science 285: 893–895. doi: 10.1126/science.285.5429.893

Thiollay JM (1993) Response of a raptor community to shrinking area and degradation of tropical rain forest in the south western Ghâts (India). Ecography 16: 97–110. doi: 10.1111/j.1600-0587.1993.tb00062.x

Trombulak SC, Frissell CA (2000) Review of ecological effects of roads on terrestrial and aquatic communities. Conservation Biology 14: 18–30. doi: 10.1046/j.1523-1739.2000.99084.x

Turner MG (1989) Landscape Ecology: the effect if pattern on process. Annual Review of Ecology and Systematics 20: 171–197. doi: 10.1146/annurev.es.20.110189.001131

Tzatzanis M, Wrbka T, Sauberer N (2003) Landscape and vegetation responses to human impact in sandy coats of Western Crete, Greece. Journal for Nature Conservation 11: 187–195. doi: 10.1078/1617-1381-00047

Underwood AJ (1994) On beyond BACI: sampling designs that might reliably detect environmental disturbances. Ecological Applications 4: 3–15. doi: 10.2307/1942110

Van Dyke FB, Brocke RH, Shaw HG, Ackerman BB, Hemker TP, Lindzey FG (1986) Reactions of mountain lions to logging and human activity. Journal of Wildlife Management 50: 95–102. doi: 10.2307/3801496

Van Langevelde F, Jaarsma CF (2004) Using traffic flow theory to model traffic mortality in mammals. Landscape Ecology 19: 895–907. doi: 10.1007/s10980-004-0464-z

Vos CC, Chardon JP (1998) Effects of habitat fragmentation and road density on the distribution pattern of the moor frog *Rana arvalis*. Journal of Applied Ecology 35: 44–56. doi: 10.1046/j.1365-2664.1998.00284.x

Watts RD, Compton RW, McCammon JH, Rich CL, Wright SM, Owens T, Ouren DS (2007) Roadless space of the conterminous United States. Science 316: 736–738. doi: 10.1126/science.1138141

Wigley TB, Roberts TH (1994) A review of wildlife changes in southern bottomland hardwoods due to forest management practices. Wetlands 14: 41–48. doi: 10.1007/BF03160620

Zhu M, Xu J, Jiang N, Li J, Fan Y (2006) Impacts of road corridors on urban landscape pattern: a gradient analysis with changing grain size in Shanghai, China. Landscape Ecology 21: 723–734. doi: 10.1007/s10980-005-5323-z

Appendix

Fragmentation metrics used to quantify the structure and the fragmentation of the road system in "Natura 2000" network.

Landscape metrics (units)†	Description
Number of fragments (none)	Equals the number of patches of the corresponding patch type (site).
Division (proportion)	Equals 1 minus the sum of patch area divided by total landscape area, quantity squared, summed across all patches of the corresponding patch type.
Splitting Index (none)	Equals the total landscape area squared divided by the sum of patch area squared, summed across all patches of the corresponding patch type.
Effective Mesh Size (km^2)	Equals the sum of patch area squared, summed across all patches of the corresponding patch type, divided by the total landscape area.

† VLATE reference