sciendo
DOI: 10.2478/jlecol-2024-0011 Journal of Landscape Ecology (2024), Vol: 17 / No. 2

QUANTIFYING THE IMPACT OF THE CONSTRUCTION OF A NATIONAL HIGHWAY ON LANDSCAPE CONTINUITY AND FRAGMENTATION OVER TWENTY YEARS – A COMPARISON OF THREE SPATIAL APPROACHES

ALONA HAIM[1*], NOAM LEVIN[1,2]

[1]*Department of Geography, The Hebrew University of Jerusalem, Jerusalem 91905, Israel*
[2]*Earth Observation Research Center, School of the Environment, University of Queensland, St Lucia, QLD 4072, Australia*
[*]*Corresponding author email: alona.haim@mail.huji.ac.il*

Received: 16th April 2024, **Accepted:** 4th August 2024

ABSTRACT

Construction and paving of road infrastructures is on the rise globally. Roads have many negative impacts on the environment, including changes and damages to landscape connectivity, fragmentation and disrupting of ecological corridors, loss of habitats, air pollution, noise pollution and light pollution. Here we aimed to examine the impacts of the construction of a major road (national Highway 6 in Israel, 188 km long) on landscape fragmentation. To this end we mapped the land cover at three-time steps: 1997 (before the construction of the road began), 2009 and 2019, quantifying both patch-based metrics (using Frgastats), the continuous metrics of landscape connectivity (using Circuitscape) and landscape continuity, adapting a before-after-control-impact methodology. Analyzing changes in those metrics for sections of the road based on their time of construction and on the distance from the highway, we found that most changes took place within a distance of up to 1 km from the new highway, starting after road construction began. We also found that the patch-based metrics and the continuous metrics were weakly correlated. We conclude that each of those different approaches has its merits and limitations, that they are complementary and that jointly they provide us with better understanding of landscape changes.
Keywords: Landscape changes, Highway, Road construction, Habitat fragmentation, Landscape continuity, Circuitscape, Ecological corridors

INTRODUCTION

The impacts of roads on landscapes

Road systems and other network structures have extensive impacts on landscape and natural areas. Road networks can change original land patterns, damage, and disrupt the spatial connectivity of the landscape (Forman & Alexander, 1998; Tinker, 1998). Road infrastructure might disrupt natural landscape processes, lead to extensive damage and loss of natural and open areas and their continuity (Fearnside, 2015; Laurance *et al*., 2009) (Tsunokawa & Hoban, 1997), and cause changes in the composition of the land cover and vegetation (Angold, 1997). In addition, roads can affect the quality of surface water sources and of underground water reservoirs (Forman & Alexander, 1998; Tsunokawa and Hoban, 1997), affect fire spread patterns (Harrington & Sanderson, 1994) or cause the loss of productive agricultural lands (Song *et al*., 2016). Moreover, vehicle traffic on roads might cause chemical pollution of natural areas and vegetation (Detwyler, 1971; Zohar *et al*., 2014) and create disturbances such as 'light pollution' and 'noise pollution' (Longcore & Rich, 2004; Slabbekoorn, 2019).

The development of transportation infrastructure and roads has been identified as one of the main factors that create "significant impact, pressure, and threat on biodiversity" (Trombulak & Frissell, 2000). Furthermore, road infrastructure constitutes a driver of habitat loss for wildlife species (Bruschi *et al*., 2015; Geneletti, 2003, Geneletti, 2006), when certain species with high area demands are most prone to be adversely impacted (Karlson & Mörtberg, 2015). Habitat loss is defined as a decrease in the size/spatial extent of the natural habitat area, even more so when the habitat becomes detached and isolated from its natural environment (Fahrig, 1997).

Moreover, road infrastructure network constitutes one of the most significant disturbance and threat factors for fragmentation of natural habitats (Forman & Alexander, 1998; Forman *et al*., 2003; Heilman *et al*., 2002; Laforge *et al*., 2022; Spellerberg, 2002;). Habitat fragmentation is the process in which a large area of habitat has been divided and split into smaller parts of the remnant habitat, becoming isolated from one another, and separated by altered land cover due to human caused land use changes (Lindenmayer & Fischer, 2013; Wilcove *et al*., 1986; Saunder *et al*., 1991). Road construction and transportation infrastructure cause to the division and splitting of the territory and create physical barriers to the movement and passage of wildlife (Gerlach & Musolf, 2000; Ahiron-Fromkin, 2012). This influence is defined as the 'barrier effect', leading to fragmentation of species and populations and causing demographic and genetic damage in the wild animals (Forman & Alexander, 1998; Forman *et al*., 2003). The more fragmented and divided is the landscape, the greater the chance that its natural ecological functions will decrease and become more disturbed (Fahrig, 1997). The effects of fragmentation and the barriers, can affect the home ranges of wildlife and decrease the connectivity of the landscape (Fu *et al*., 2010; Poessel *et al*., 2014).

An increase in road density results in an increase in landscape fragmentation (Hawbaker, 2006), and relates with habitat loss and habitat fragmentation, with roads expansion significantly increasing the rate of the fragmentation (Shirvani *et al*., 2020). Road extent and road length were found to be a critical factor explaining bird species richness (Konstantopoulos *et al*., 2020).

Habitat fragmentation and habitat loss usually occur in parallel and are related to each other (Fahrig, 1997, 2003; Haddad *et al*, 2015), and are considered to be one of the main drivers of species extinction worldwide (Fahrig, 1997; Brooks *et al*., 2002). When road infrastructure separates and divides a contiguous population of a species into smaller local populations, there is a higher probability of their extinction (Vos & Opdam, 1993).

Quantifying landscape fragmentation

Fragmentation metrics aim to quantify the level of landscape fragmentation, i.e., the transformation of a contiguous patch of habitat into several smaller, convoluted, and disjunct patches, isolated from each other by a matrix of habitat unlike the original. Fragmentation metrics can be computed at the landscape, class or patch level. This approach became widely used with the introduction of the FRAGSTATS software (McGarigal, 1995), which allowed the calculation of a wide range of metrics, relating to the area, core area, shape, isolation/proximity, contrast, contagion, connectivity, and diversity of landscape patches (to name a few of the metrics; Kupfer, 2012). However, this approach requires the landscape to be first divided into habitat classes (i.e., it cannot be calculated for a continuous conceptualization of landscapes; Bruton *et al*., 2015), and it does not provide spatial outputs to facilitate the visualization of areas with high or low fragmentation.

Several alternative approaches have developed since. The landscape continuity approach (Levin *et al*., 2007), assigns a continuity value to open landscape grid cells, as a function of their weighted distance from different types of built areas, which are weighed based on their estimated impact on surrounding open landscape areas. Open landscape areas are defined as areas that are not covered with permanent structures such as buildings or roads (Costanza *et al*., 1997). Therefore, natural areas, semi-natural and agricultural areas are called 'open areas' or 'open landscape areas' (Kaplan & Slotsky, 2002). When these open-landscape patches are adjacent, the continuity of the open landscape is higher, regardless of the type of the natural habitat (Levin *et al*., 2007). This approach provides output maps of landscape continuity and allows to calculate changes in landscape continuity over time.

A more recent approach which has gained popularity in the quantification of landscape connectivity is based on concepts borrowed from electric circuit theory, where flow rates are quantified and visualized based on landscape resistance (or conductance; McRae *et al*., 2009; Dickson *et al*., 2019). The Circuitscape software can be operated in several modes and provides the users with output maps showing cumulative flux measures, indicating possible pathways between habitat patches, bottlenecks, and link redundancy (Rayfield *et al*., 2011; McRae *et al*., 2016).

Researchers often choose one of the above approaches (or other similar approaches), but usually do not conduct a comparison between different approaches for mapping changes in landscape fragmentation/continuity/connectivity.

Research aims

Following land use changes which started in the late 19th century, the natural habitats in Israel's Mediterranean climate zone are very fragmented (Schaffer & Levin, 2014), and there are several highways crossing Israel's Mediterranean landscape. In addition, the Separation Wall between the State of Israel and the Palestinian Authority, creates an additional buffer that disrupts the continuity of the natural areas impacting the connectivity of the habitat (Yom-Tov *et al*., 2020).

In this study, we had several main objectives: First, we wanted to quantify the impact of a major highway on landscape fragmentation and continuity. Our additional objective was to compare three different spatial analysis methods for assessing distinct aspects of what is collectively termed as 'landscape fragmentation' - 'classic' fragmentation metrics, landscape continuity and landscape connectivity.

For our case study, we focused on the impacts of the national Highway 6 in Israel (`Trans-Israel Highway`), which cuts the country lengthwise, connecting most of Israel's urban areas. The study seeks to examine the possible impacts of this highway on landscape fragmentation and continuity during the construction and operation of Highway 6 between the years 1999-2019. The spatial analysis examines a long period of more than 20 years (the years 1997, 2009 and 2019), which refers to the period before the road was built and during the development and operation of its construction, allowing us to examine the impacts of this major road on the landscape both spatially and temporally over the past 20 years.

We hypothesized that the construction of Highway 6 caused the acceleration of fragmentation processes in the open areas around the road, because of the road infrastructure construction and the processes of expanding construction that the road facilitated in its vicinity. Moreover, we hypothesized that changes in the continuity and connectivity of the open areas will decrease with distance from Highway 6.

MATERIALS AND METHODS

Study area

This study focuses on the Highway 6 in Israel which is also known as the 'Trans-Israel Highway'. This road is Israel's major highway, which stretches from the north of Israel to the south, with a current length of approximately 188 km. The construction of Highway 6 began in 1999, and every few years additional sections of the road have been opened (see Fig. 1; Tables S1, S2).

For our analysis, we divided the road into 23 sections (between major interchanges). Each of these sections has a different length and was constructed and opened for use in a different year (www.kvish6.co.il, accessed 2022, April 1). Then, we created a buffer around the road and divided it to 23 sections that include west and east sides, hence altogether we created 46 sub-areas. In addition, we created buffers of 1, 2, 3, 4, 5 and 8 km from the road to the east and west sides, thus allowing us to examine changes in landscape fragmentation, connectivity and continuity as a function of the distance of the road (see Fig. 1). The maximum buffer size of this study area (8 km) was chosen due to the need to test enough distance units from the highway. On the east side from the highway the buffer area included parts of the separation-wall between Israel and the West Bank (which was built and changed over those years), however we did not want to extend too much further eastwards into the West Bank where land cover and land use dynamics are quite different than within the State of Israel. On the west side, we wanted to include a significant area containing part of cities of the Israeli coastal plain that have developed greatly over the years, without extending into the Mediterranean Sea, which in some sections is only 9-11 km away, and without including major coastal cities, such as Haifa, Netanya, Tel-Aviv etc., for which the development of Highway 6 will not have much of an impact (in terms of the fragmentation of open landscapes).

To follow temporal changes in landscape fragmentation/continuity/connectivity, we used the following three points in the time to follow changes in the open landscapes over two time periods: the time preceding the construction of Highway 6 (the year 1997- the time before land expropriation in favor of the road or actual road construction began), an intermediate year after some of the road sections have been opened (the year 2009), and a time after all the 23 road sections have been opened (the year 2019). The area that was included in the study includes 8 km to the east and 8 km to the west of Highway 6, where the total area investigated around the road was 3,038 square kilometers (almost 14 % of the area of the State of Israel).

Data sets

In order to examine spatial changes in land cover that took place, we created land cover maps for three years 1997, 2009 and 2019. The classification of the area included the following land cover classes: built-up areas (by categories: roads, railway lines, settlements, agricultural buildings, industrial areas, quarries and mining waste, earthworks, solar energy facilities), and open areas, using the following categories: batha (small shrubs and herbaceous vegetation) and shrubland areas, Mediterranean maquis and planted forests, agricultural areas, and water bodies. To achieve this, a comprehensive and extensive digitization of maps and satellite images was done using various sources, such as high-resolution orthophotos (at a spatial resolution of 1 m from the Survey of Israel), Landsat satellite images, GIS layers, atlases, topographic maps, and road guides.

Fig. 1: The Sections of Highway 6 and their names. Road sections are colored according to the year of development of Highway 6 and the lateral roads built along with it. The research polygons, the 23 sections and the buffer zones (of 1, 2, 3, 4, 5 and 8 km) that we used to analyze possible impacts of the road on landscape fragmentation are shown in grey.

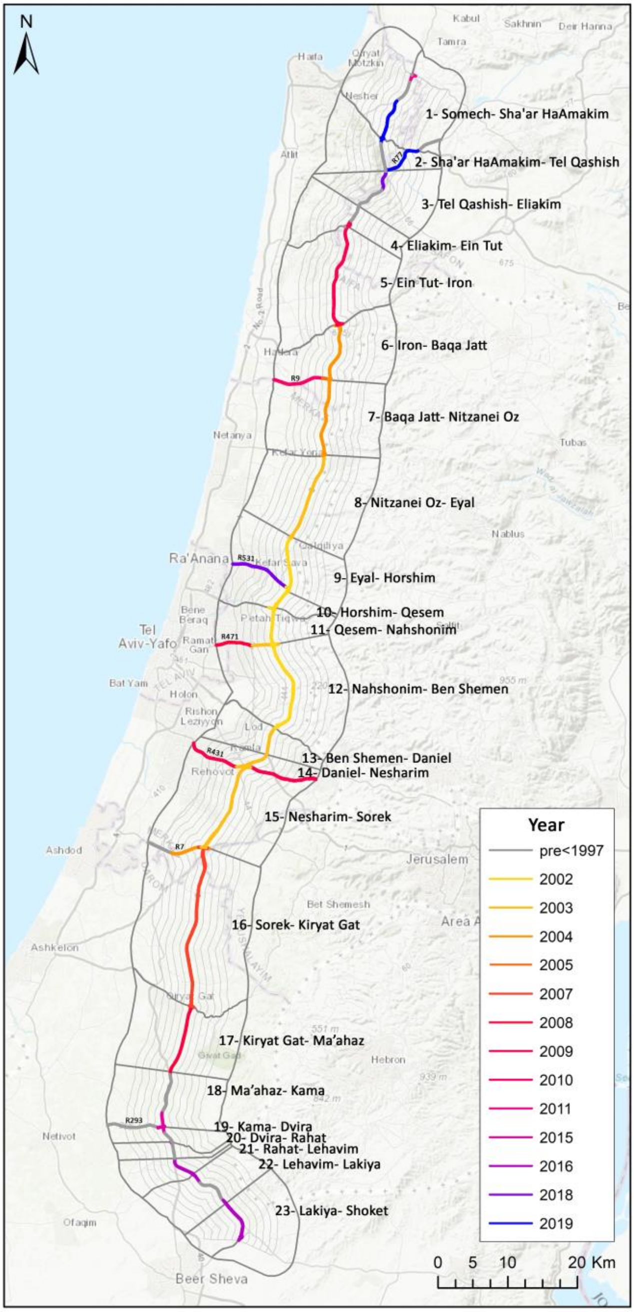
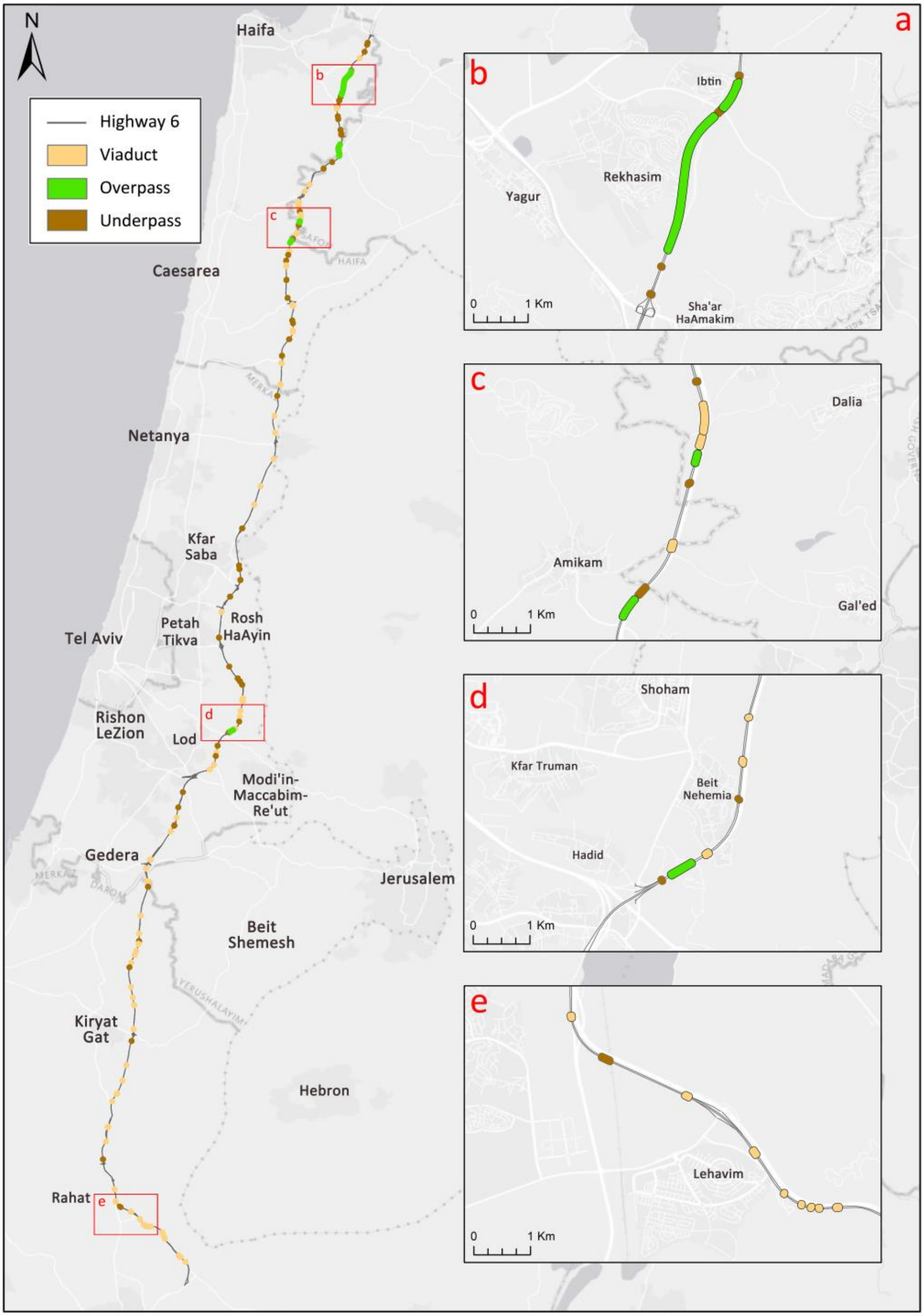


Fig. 2: Wildlife crossings by their different types along Highway 6: Viaducts (e.g., bridge over a river), Overpasses (i.e., tunnels) and Underpasses (e.g., where a local road goes under the highway; a- all the crossings in the research area; b,c,d,e- zoom-in to selected crossings along highway 6).



The various sources of data which were used for our digitization (for the years 1997, 2009 and 2019) are summarized in Tables S3 and S4. In all the different analysis that were done, the land cover layers were raster, with the size of the raster cell being 25x25 meters (the land cover for the years 1997, 2009 and 2019 were first mapped in vector form and then converted to raster layers); Only the Circuitscape analysis was run at a coarser spatial resolution of 100 m, due to the much longer run time of this algorithm.

In order to include the contribution of tunnels and underpasses to landscape continuity and connectivity, we also mapped all tunnels and underpasses (over rivers or other roads) using remote sensing (mapping based on a visual interpretation of satellite images and orthophotos) with some of the tunnels and underpasses also derived from existing GIS layers. Along Highway 6 there are six tunnels, where one of them was explicitly built as a designated ecological crossing (wildlife crossing; Fig. 2). We mapped and classified all these potential wildlife crossings into three different types (overpass, underpass, and viaduct; Denneboom *et al*., 2021).

Spatial analysis

We applied four different analysis approaches to examine the changes that took place following the construction of Highway 6:

Changes in percent cover of different classes **-** This includes an analysis of the changes that have occurred in land cover classes, such as the conversion from open areas to built-up areas.

Habitat fragmentation **-** In order to quantify habitat fragmentation, we divided the non-built areas into three land cover classes: batha (small shrubs and herbaceous vegetation) and shrubland areas, Mediterranean maquis and planted forests, and agricultural areas. We used the *Fragstats* tool, which examines the changes in the structure of the landscape and the fragmentation scope of the habitats. We calculated the following fragmentation metrics for each of three open areas classes, for each of the years (1997, 2009 and 2019), within each of the 46 sub-sections:

- Total area - the total area occupied by the habitat within a section.
- Percentage of Landscape- the relative percentage occupied by each habitat within a section.
- Patch Area - the average size of the patches that make up the habitat within a section.
- Number of patches within a section.
- Total Edge - the total length of the margin of the patches that make up the habitat within a section.
- Total Core Area - the total size of the core habitat areas within a section, defined as areas within a distance of 200 m from the edge of the habitat; Low values represent less core and a higher degree of fragmentation, while high values represent more patch core and a lower level of fragmentation.
- Percent Core Area - the ratio between the total core area and total habitat area within a section. Lower values represent greater fragmentation.
- Euclidean Nearest Neighbor Distance - the average distance between a patch and the closest patch of the same class within a section.

Changes in landscape continuity **-** we used the approach developed by Levin et al. (2007) to quantify changes in landscape continuity between the years 1997, 2009 and 2019. To map landscape continuity, we classified the built-up areas and assigned each of the classes of the built-up areas with a relative impact weight following Levin *et al*. (2007; Table 1; Fig. S1). We calculated the distance of each grid cell (at a spatial resolution of 25 m) from the nearest built-up area for each built-up class, separately. We then multiplied these 'distance surfaces' by the inverse of the weight of each category, and we created the landscape continuity map for each period, by calculating the minimum value of the weighted distance surfaces in a grid cell (Levin *et al*., 2007). we calculated changes in landscape continuity based on the differences in landscape continuity between 1997, 2009 and 2019.

Table 1: The weights given to the categories of built-up areas for the landscape continuity analysis (Section 2.3.3), and the Cost-distance weights assigned to the land cover classes for the Circuitscape analysis (Section 2.3.4).

Category type	Weight of built-up areas for the landscape continuity analysis	Cost-distance weights for calculating the connectivity of the heterogeneous landscape using Circuitscape
Batha and shrubland areas, Mediterranean maquis and planted forests, The areas above the tunnels and the ecological crossing	-	1
Agricultural areas, water areas	-	5
Field work of railway-line construction, quarter roads, agricultural buildings	25	25
Dirt roads, the railway line, tertiary roads, quarries and mining waste, earthworks, other violated land area	50	$50^{1.5} = 354$
Secondary road	75	$75^{2} = 5625$
Highway 6, the Separation Wall, lateral roads built with highway 6, Primary roads, built-up area (settlements), industrial area, other traffic violated area, solar energy facilities	100	$100^{2.5} = 100{,}000$

* All the roads in the study area were classified and ranked according to road size, number of lanes, whether it was a highway or a local road, whether it had separation fences, etc.

Changes in the connectivity of the heterogeneous landscape - We used *Circuitscape* to quantify changes in landscape connectivity between 1997, 2009 and 2019, and to identify potential bottlenecks for wildlife movement. Based on the land cover maps, a "cost distance" surface was created (at a spatial resolution of 25 m), for which we assigned the open-area categories weights according to environmental considerations (grid cells were coded with resistance values, representing the ability of species to pass; Table 1). To quantify the connectivity of the heterogeneous landscape, we randomly distributed 1,042 points over the categories of open areas (Table 1- categories with weights 1 and 5). The selected run mode was ‘All to one’, and the output layer that was chosen on Circuitscape is ‘current map’ (this outcome allows to identify areas which contribute the most to the connectivity between the heterogeneous landscape (McRae *et al*. 2008). This analysis was run at a spatial resolution of 100 m due to the longer time to run this algorithm.

Statistical analysis

We examined changes in the variables which we calculated and described above, between the years 1997-2009-2019, while testing whether these changes were impacted by the distance from the road or by the time since the construction time of the road sections. For that, we examined the effect of the road as a function of the distance from Highway 6, using the following distance classes to the east and west sides of the road: 0-5 km, 0-8 km, 0-1 km, 1-2 km, 2-3 km, 3-4 km, 4-5 km, and 5-8 km.

This study uses the before-after-control-impact (BACI) analysis method (Smith *et al*., 1993). With this method, the sites disturbed by human influence (impact) are compared with sites that were not disturbed (control), before and after the human interference. This study examines the area surrounding Highway 6 before and after its sections were built. Since in each period of time there were sections that have already been built and other sections that have not yet been built, it would be possible to distinguish and compare disturbed areas where the road section has already been built and undisturbed areas where the road has not yet been built. When a difference is found in the environmental variable being examined and an effect is found depending on the time variable related to the construction of the road section, this would be strong evidence that human intervention has caused a change in the area (Roedenbeck *et al*., 2007).

In order to apply the BACI analysis, we classified the 23 segments into three groups with a common factor - the period in which the sections were built (Table 2). This division allowed us to examine the situation prior to the construction of each section of the road, and the situation after its construction, to compare between the different sections' groups, and to test whether there were differences in the values of the metrics between those years.

Table 2: Division of Highway 6 sections into groups based on the time of their construction

Group name	**Sections**
Sections built between 1999-2009	4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17
Sections where part of the section existed in 1997 and the other part was built between 2010-2019	1, 2, 3, 18, 19, 20, 22
Sections built between 2010-2019	21, 23

We ran the ANOVA test with JMP Pro 16 software to examine the statistical distributions of the values of the different landscape fragmentation metrics for the years 1997, 2009 and 2019, and to test whether they varied between sections as a function of the time a road section was built and as a function of the time it was built.

In order to examine the complementarity and similarity between the different landscape fragmentation metrics, we calculated Spearman correlation matrices between all fragmentation metrics (those derived from Frgastats, the landscape continuity and Circuitscape). The correlations were calculated between the values of the metrics within each section (n = 46) within a buffer zone of 8 km from Highway 6, for the three time periods (n = 3), i.e., for a sample size of n = 138.

RESULTS

Changes in land cover

Several new neighborhoods and towns developed in close vicinity to Highway 6 between the years 1997 and 2019. Of special notice are (from north to south) the new town of Harish, new neighborhoods in Rosh Ha'Ayin, the new town of El'ad, the industrial park of Modi'in near Shoham, new neighborhoods in Yad Binyamin, Kiryat Gat and Lehavim (Fig. 3; Fig. S2).

We found that statistically significant changes in built-up area class between the road's sections (grouped based on their construction period), only occurred within 0-1 km from Highway 6 (Fig. 4), with changes being statistically significant only for the group of segments built between 1999-2009. For road sections which were built after 2010, while there was an increase in built-up areas, these changes were not statistically significant (Fig. 4).

Examining changes in built-up areas a function of the distance from highway 6, there was a trend of gradual moderation in the change that has occurred in the built-up area. At a distance greater than 1 km, although there was a certain change in the built-up area, we did not find any statistically significant change as a function of the time since the highway was built.

Habitat fragmentation

When we focused on the changes that occurred in the land cover classes at a distance of 0-1 km from highway 6, we found that they were greater in size compared to the changes that occurred at a distance of 0-8 km (Table 3). It can be understood that the main changes occurred in the range of the area closer to Highway 6. Along most of the length of Highway 6, natural vegetation classes were more abundant to the east of Highway 6 than to the west of it (Fig. 5).

Table 3: The percentage of the land covered by open space habitats and built-up distances of 0-1 km and 0-8 km from Highway 6, in the years 1997, 2009 and 2019.

0-1 km	**1997**	**2009**	**2019**
Batha and shrubland	11.2%	9.8%	8.86%
Mediterranean maquis and planted forests	13.4%	12.7%	12.4%
Agricultural areas	58%	52.3%	49.4%
Built-up areas	17.4%	25.2%	29.34%
0-8 km	**1997**	**2009**	**2019**
Batha and shrubland	17.1%	16.2%	15%
Mediterranean maquis and planted forests	15%	14.9%	14.5%
Agricultural areas	46.9%	45.3%	42.9%
Built-up areas	21%	23.6%	27.6%

Fig. 3: The development of the built-up area in the study area throughout the years. See additional zoom-in maps in Fig. S2 (a-the change in the entire research area; b-zoom-in to sections 6-11).

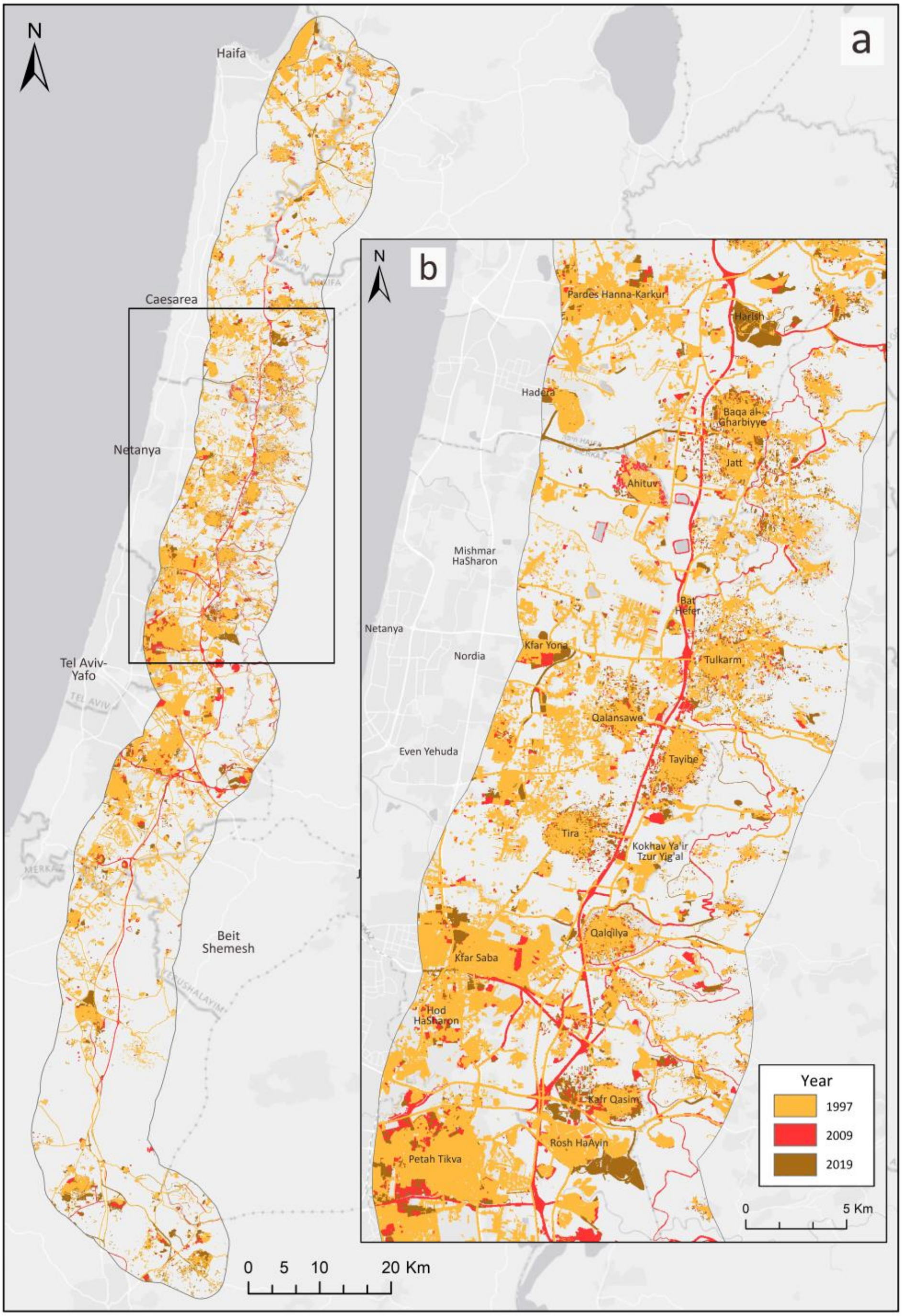
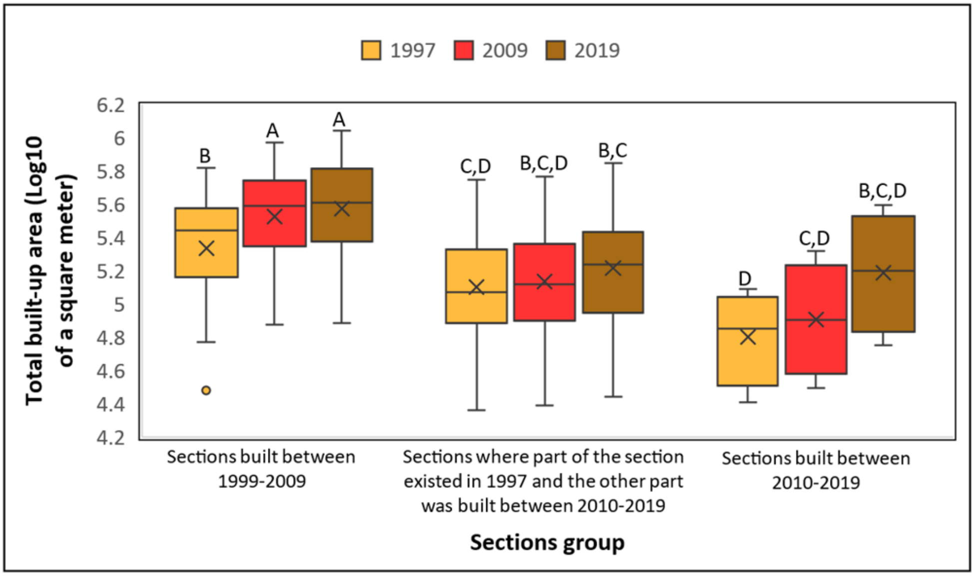


Fig. 4: The distribution of the built-up area in the years 1997, 2009 and 2019 at 0-1 km from Highway 6, for the sections of Highway 6. P<0.0001, N=138 (sample size- the three years 1997, 2009 and 2019 and the 46 research areas)

Categories not sharing the same letter were significantly different in their total built-up area, based on an ANOVA test. The letters above each graph refer to the average statistical value of the connectivity of the heterogeneous landscape for each year (in each section group). Box plots not sharing the same letter had statistically significant differences in their mean value.



Changes in landscape continuity

Highway 6 was developed along the coastal plain of Israel where the density of roads and built-up areas was already relatively high, however some of the sections of this highway, especially in the north and south, contained relatively large areas of open spaces (Fig. 6). Generally, we found that landscape continuity decreased with time within a distance of 0-1 km from Highway 6 – this happened earlier for road sections built between 1997-2009, and later for road sections built between 2010-2019 (Fig. 7). At distances greater than 2 km from Highway 6 we found no statistically significant decreases in landscape continuity over the time period we analyzed. Most of the decreases in landscape continuity between 1997 and 2019 took place east of Highway 6 (Fig. 8), where the extent of open spaces was initially higher (Fig. 5).

Fig. 5: Changes that took place between the years 1997, 2009 and 2019 in the habitats and open landscape in the study area, leading to increased fragmentation and conversion of habitats into built-up areas

(a- the entire area in 1997; d- zoom in 1997; b- the entire area in 2009; e- zoom in 2009; c- the entire area in 2019; f- zoom in 2019).

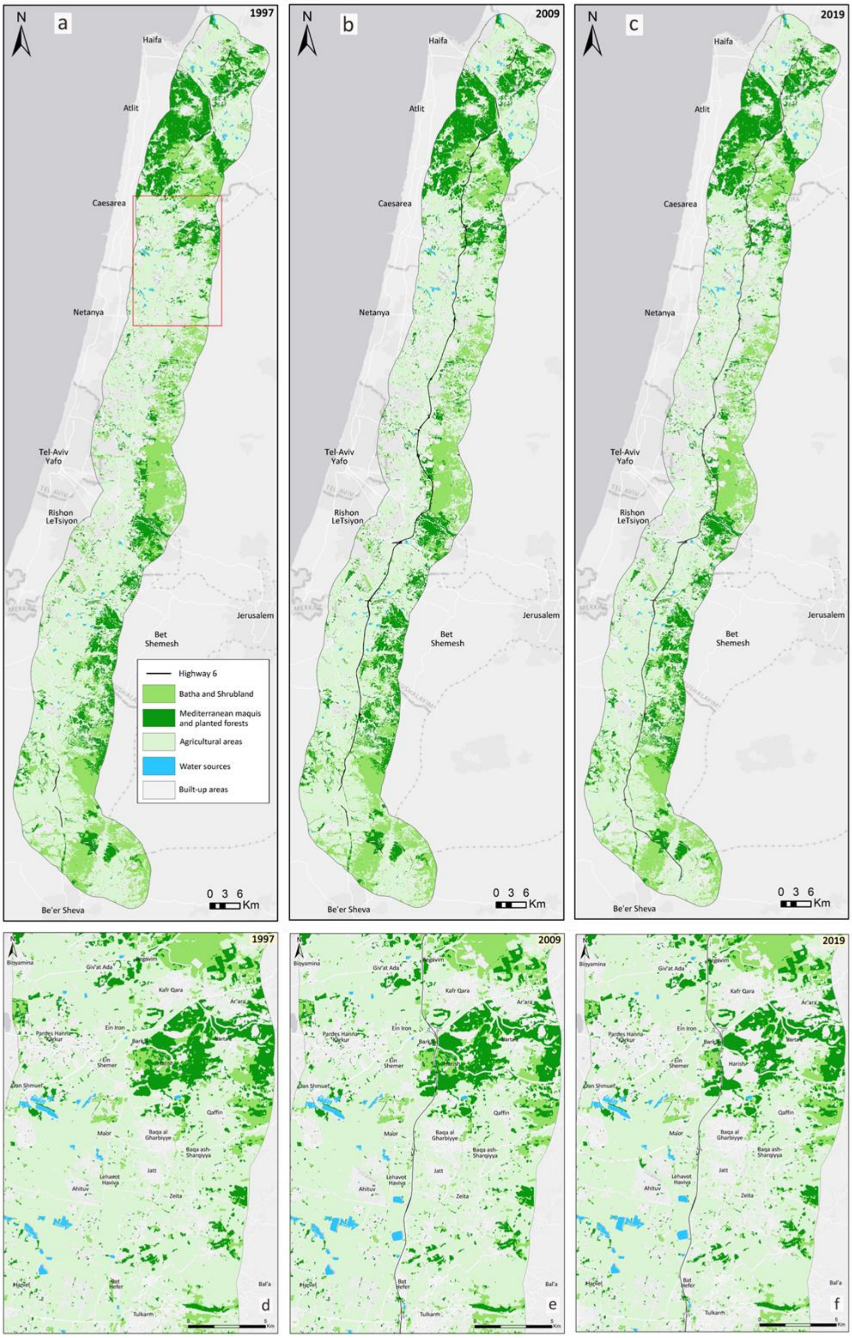


Fig. 6: Maps showing landscape continuity in the years 1997, 2009 and 2019, demonstrating change created by Highway 6 during those years

(a- the entire area in 1997; d- zoom in 1997; b- the entire area in 2009; e- zoom in 2009; c- the entire area in 2019; f- zoom in 2019).

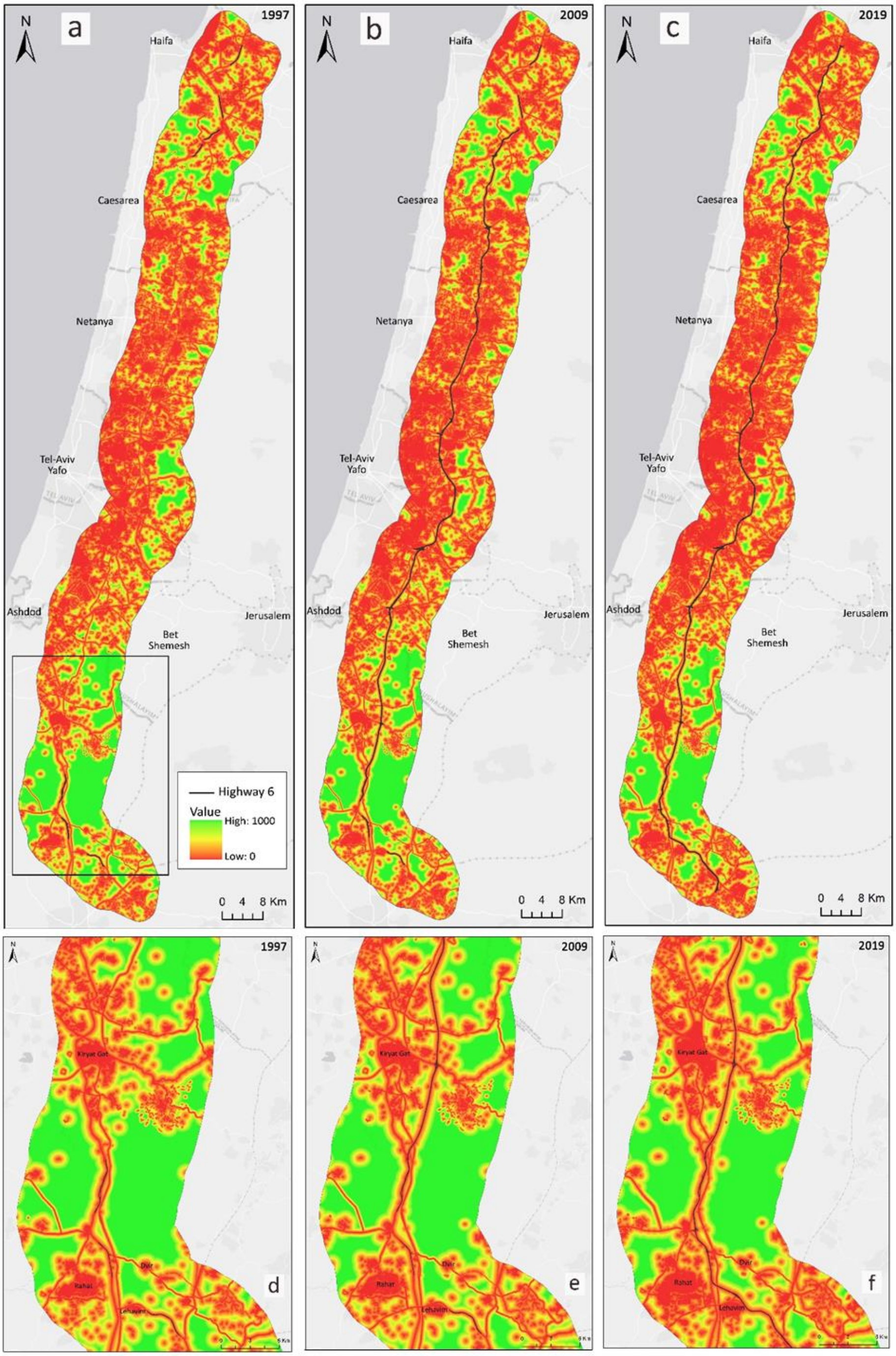
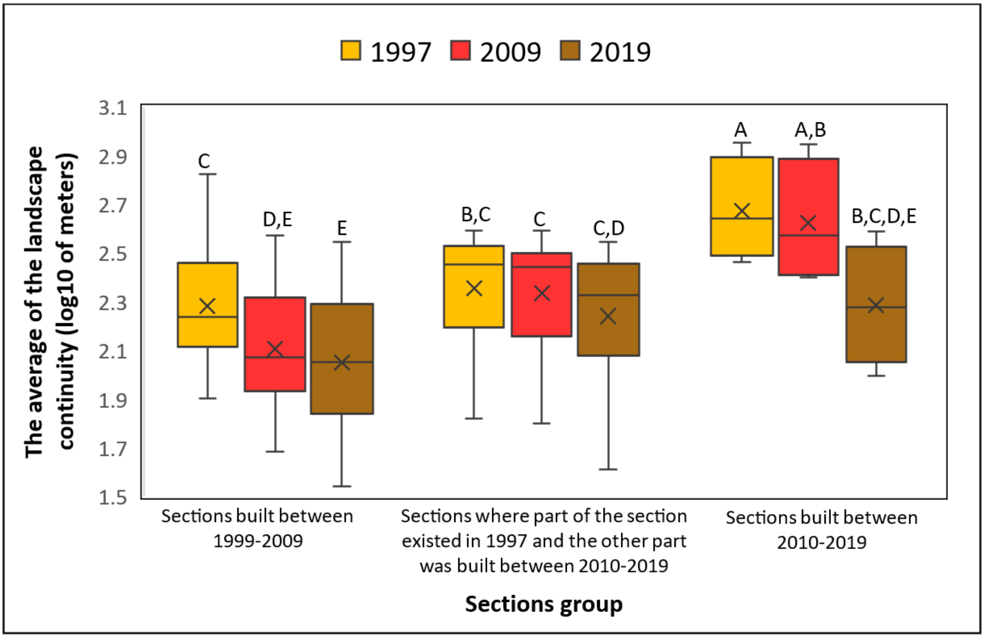


Fig. 7: The values distribution of average of the landscape continuity in the years 1997, 2009 and 2019 at 0-1 km from Highway 6, for the sections of Highway 6. P<0.0001, N=138

(sample size- the three years 1997, 2009 and 2019 and the 46 research areas). Categories not sharing the same letter were significantly different in their average landscape continuity, based on an ANOVA test.

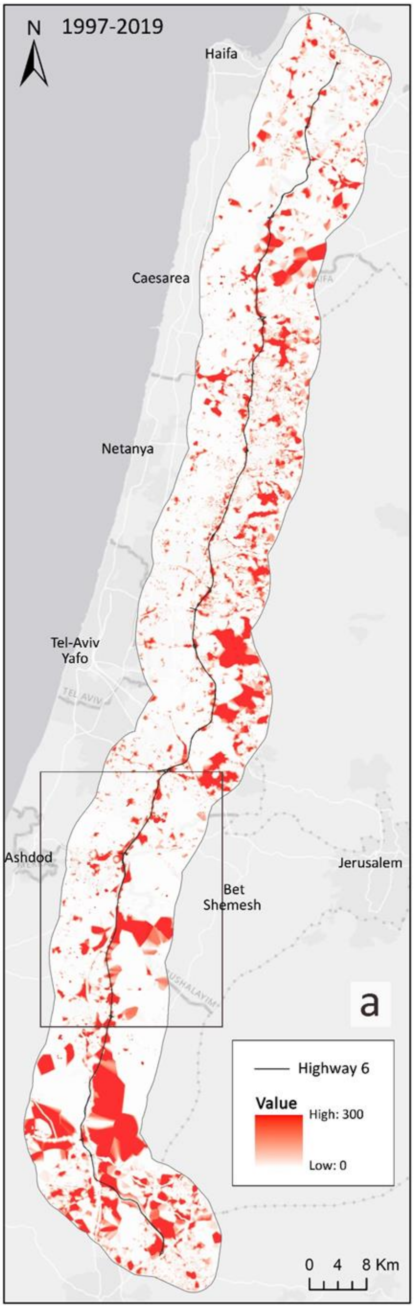


Changes in the connectivity of the heterogeneous landscape

The connectivity analysis using Circuitscape highlighted the importance of the areas east of Highway 6 as critical for allowing the potential movement of animals between habitats, especially in the central areas of Highway 6, where open spaces are scarcer (Fig. 9). The importance of the areas east of Highway 6 has increased between 1997 and 2019, as many areas which served as potential corridors in 1997, have become less conducive for wildlife movement between habitat patches (Fig. 10). An example for changes in landscape connectivity can be given for the ecological overpass of 'Dalia' (located in section no. 5 of Highway 6). This overpass became a critical area for maintaining landscape connectivity after the road section was paved, becoming a bottleneck and a necessary focal point for maintaining landscape connectivity on both sides of Highway 6 (Fig. S3). At a distance up to 1 km from Highway 6, for the group of the sections which were built between the years 1999-2009, we found a significant decrease in the values of the connectivity of the heterogeneous landscape between the years 1997-2009 (Fig. 11). We did not find statistically significant changes in the connectivity values over the years for sections which were built after 2010. At distances greater than 1 km from Highway 6 we did not find statistically significant changes in the connectivity values as a function of the time that the road section was built.

Fig. 8: The difference (the total damage of the landscape continuity), showing the changes in the values of the landscape continuity in the Highway 6 area between the years 1997 and 2019

(the values representing this expression: 1997-2019; a- the total damage in the entire research area; b- zoom-in to sections 15-16)



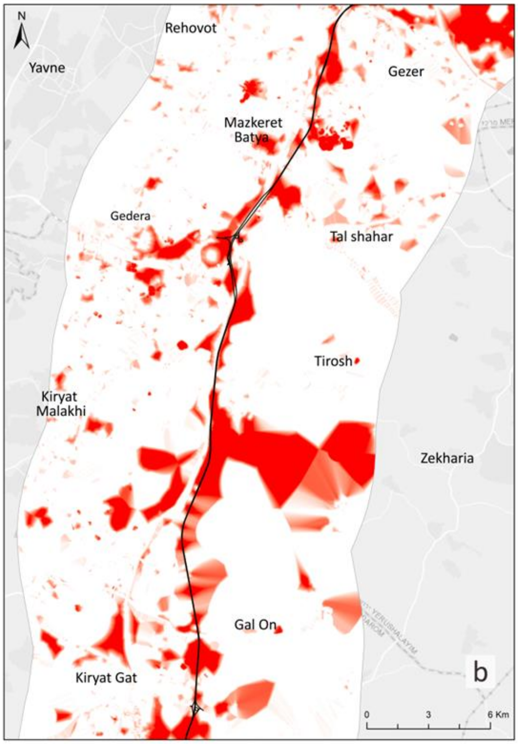


Fig. 9: Connectivity maps derived from Circuitscape. The study area is described as a surface that allows the conduction of current, that is, the potential of animals to pass between habitats and the open areas.

High values (yellow) express bottlenecks, i.e., areas with a higher value for maintaining the connectivity of the heterogeneous landscape ((a- the entire area in 1997; d- zoom in 1997; b- the entire area in 2009; e- zoom in 2009; c- the entire area in 2019; f- zoom in 2019).

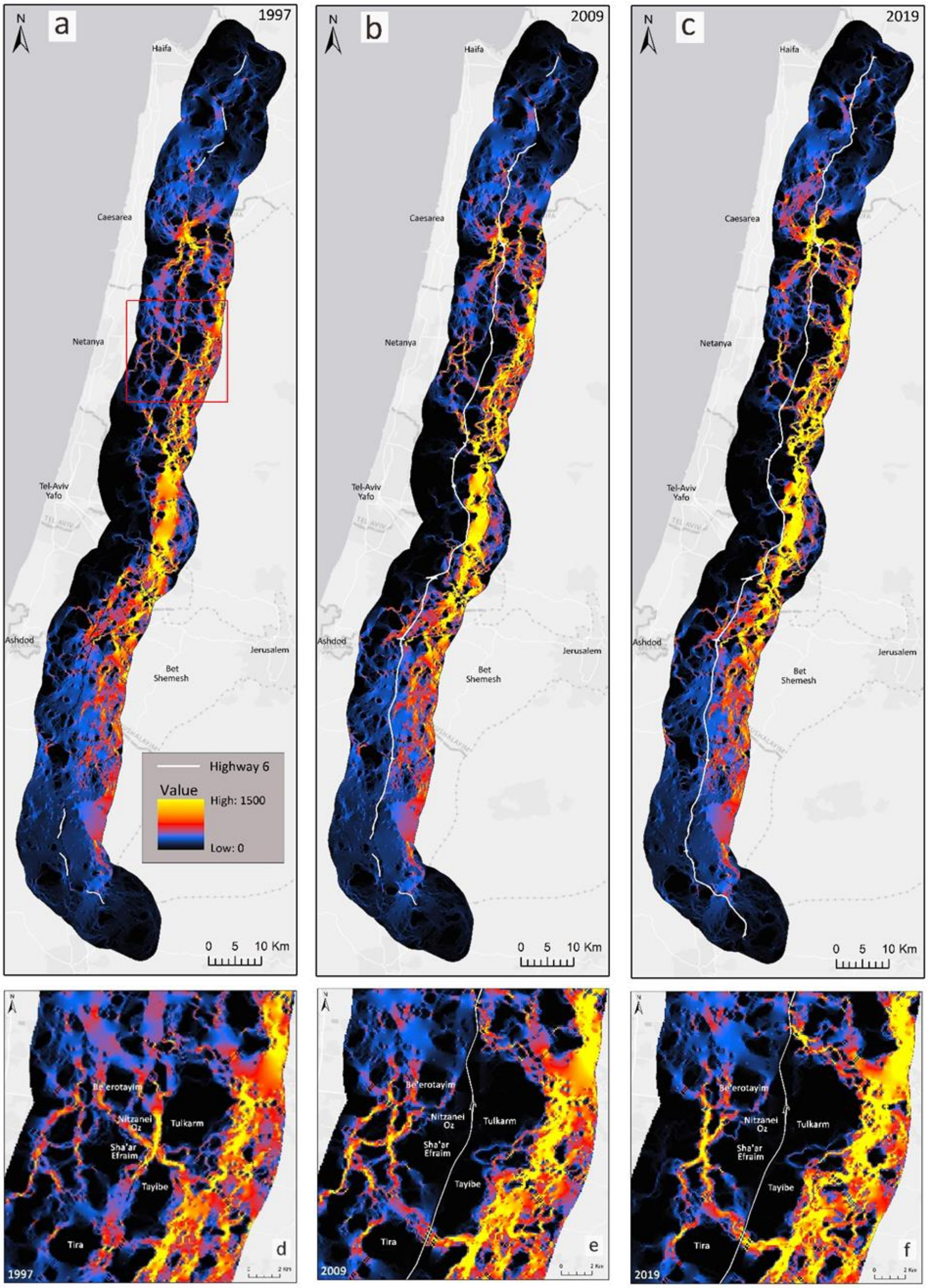
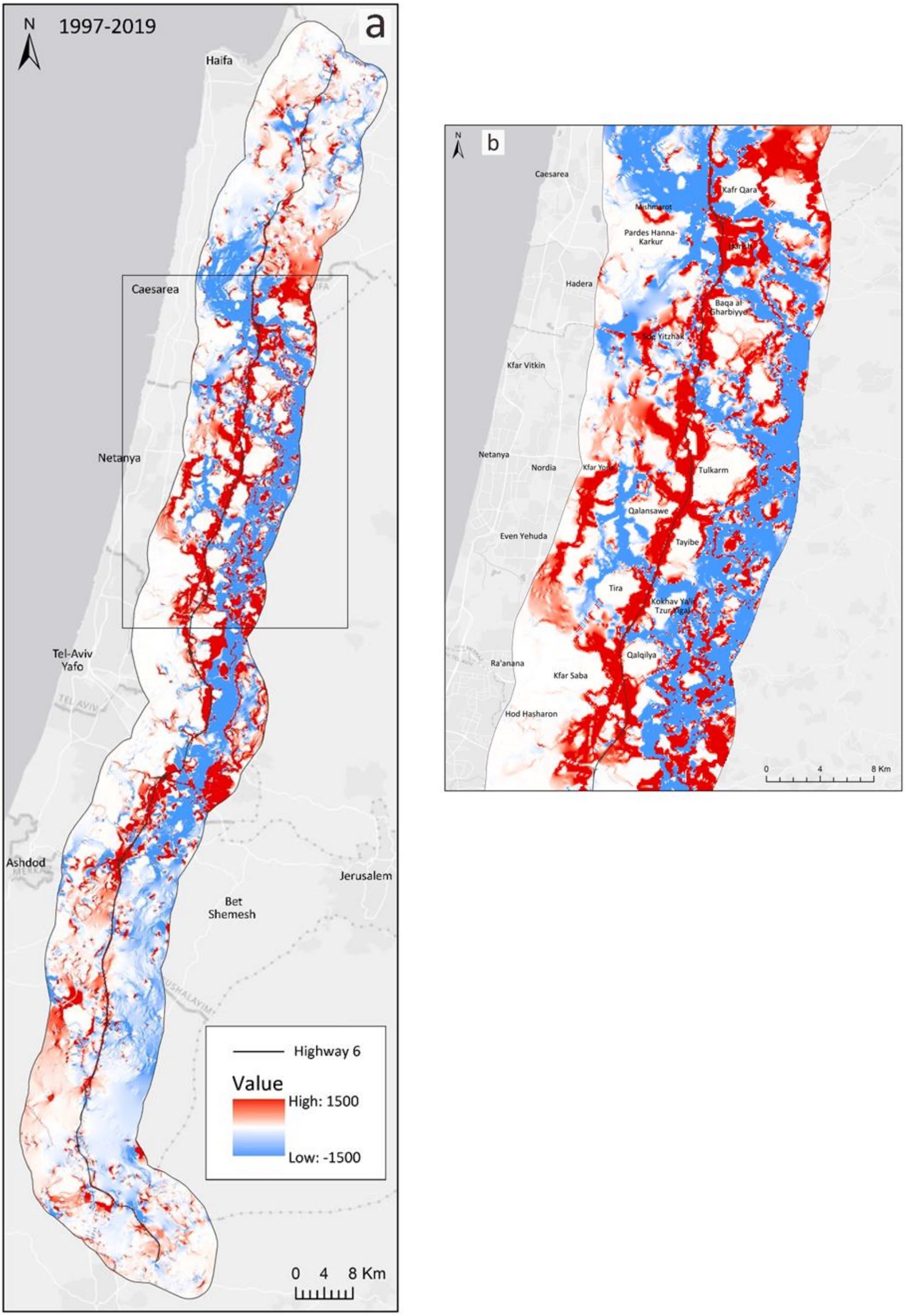


Fig. 10: Changes in the connectivity of the landscape between 1997 and 2019.
High positive values (red) represent areas where the connectivity of the heterogeneous landscape has severely decreased between the years 1997-2019, and blue areas (negative values) represent areas whose importance as essential corridors has increased (a- the change in the entire research area; b- zoom-in to sections 6-10).



Comparison between the different approaches for quantifying landscape fragmentation, continuity, and connectivity

Overall, the correlations between the different metrics were highest within the batha and shrubland areas (median $R_s^2 = 0.291$), followed by the Mediterranean maquis and planted forest areas (median $R_s^2 = 0.173$) and the agricultural areas (median $R_s^2 = 0.094$) (Tables 4, 5, 6). The metrics of landscape continuity and landscape connectivity were not correlated with each other, and presented low correlations ($R_s^2 < 0.5$) with all other metrics, within each of three open landscape classes (batha and shrublands, Mediterranean maquis and planted forest, and agricultural areas) (Tables 4, 5, 6). The fragmentation metrics which showed the highest pairwise correlations ($R_s^2 > 0.5$) within the batha and shrubland and the maquis and forest areas were the "Percentage of the total landscape", "Total class area" and "Percentage of open landscape".

Fig. 11: Average connectivity of the heterogeneous landscape in the years 1997, 2009 and 2019 at 0-1 km from Highway 6, for the sections of Highway 6. P<0.0001, N=138 (sample size- the three years 1997, 2009 and 2019 and the 46 research areas).
Categories not sharing the same letter were significantly different in their average connectivity, based on an ANOVA test

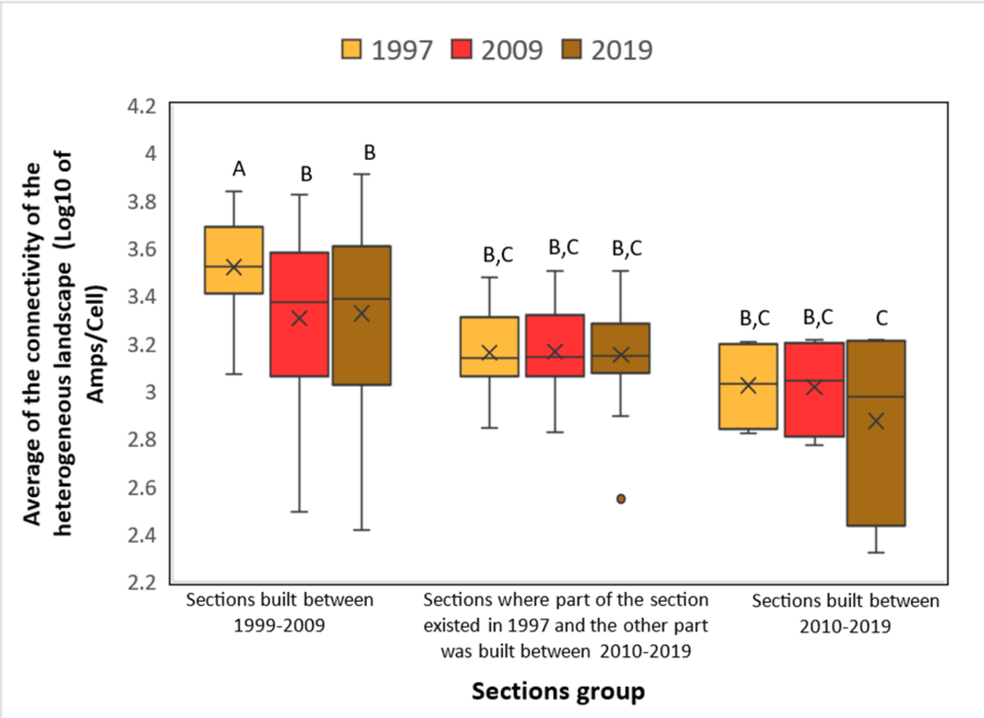


Table 4: Correlation matrix of different fragmentation metrics for the batha and shrubland areas, calculated for the 46 sections over the three time periods, within a buffer of 8 km around Highway 6 (n = 138). * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

	1	2	3	4	5	6	7	8	9	10	11	12	13
1: Number of patches		0.107	0.582 ***	0.107	0.732 ***	-0.052	0.250 **	0.188 *	-0.377 ***	0.060	0.169 *	-0.039	0.143
2: Percent of total landscape	0.107		0.816 ***	0.975 ***	0.665 ***	0.926 ***	0.845 ***	0.838 ***	-0.840 ***	0.637 ***	0.435 ***	0.477 ***	0.384 ***
3: Total class Area	0.582 ***	0.816 ***		0.802 ***	0.915 ***	0.753 ***	0.879 ***	0.837 ***	-0.783 ***	0.546 ***	0.388 ***	0.350 ***	0.322 ***
4: Percentage of open Landscape	0.107	0.975 ***	0.802 ***		0.608 ***	0.914 ***	0.832 ***	0.824 ***	-0.820 ***	0.500 ***	0.386 ***	0.313 ***	0.328 ***
5: Total Edge	0.732 ***	0.665 ***	0.915 ***	0.608 ***		0.540 ***	0.708 ***	0.649 ***	-0.756 ***	0.595 ***	0.383 ***	0.435 ***	0.330 ***
6: Patch Area - Mean	-0.052	0.926 ***	0.753 ***	0.914 ***	0.540 ***		0.884 ***	0.885 ***	-0.679 ***	0.587 ***	0.386 ***	0.447 ***	0.326 ***
7: Total Core Area	0.250 **	0.845 ***	0.879 ***	0.832 ***	0.708 ***	0.884 ***		0.992 ***	-0.648 ***	0.548 ***	0.352 ***	0.378 ***	0.275 **
8: Percent core area	0.188 *	0.838 ***	0.837 ***	0.824 ***	0.649 ***	0.885 ***	0.992 ***		-0.612 ***	0.539 ***	0.340 ***	0.385 ***	0.265 **
9: Euclidean Nearest Neighbor Distance - Mean	-0.377 ***	-0.840 ***	-0.783 ***	-0.820 ***	-0.756 ***	-0.679 ***	-0.648 ***	-0.612 ***		-0.503 ***	-0.308 ***	-0.364 ***	-0.264 **
10: Landscape continuity in batha	0.060	0.637 ***	0.546 ***	0.500 ***	0.595 ***	0.587 ***	0.548 ***	0.539 ***	-0.503 ***		0.378 ***	0.918 ***	0.344 ***
11: Connectivity of the landscape in batha	0.169 *	0.435 ***	0.388 ***	0.386 ***	0.383 ***	0.386 ***	0.352 ***	0.340 ***	-0.308 ***	0.378 ***		0.249 **	0.954 ***
12: Landscape continuity – overall	-0.039	0.477 ***	0.350 ***	0.313 ***	0.435 ***	0.447 ***	0.378 ***	0.385 ***	-0.364 ***	0.918 ***	0.249 **		0.258 **
13: Connectivity of the landscape - overall	0.143	0.384 ***	0.322 ***	0.328 ***	0.330 ***	0.326 ***	0.275 **	0.265 **	-0.264 **	0.344 ***	0.954 ***	0.258 **	

Table 5: Correlation matrix of different fragmentation metrics for Mediterranean maquis and planted forests, calculated for the 46 sections over the three time periods, within a buffer of 8 km around Highway 6 (n = 138). * p < 0.05, ** p < 0.01, *** p < 0.001.

	1	2	3	4	5	6	7	8	9	10	11	12	13
1: Number of patches		0.257 **	0.557 ***	0.280 ***	0.766 ***	-0.042	0.195 *	0.107	-0.387 ***	-0.181 *	0.260 **	-0.259 **	0.267 **
2: Percent of total landscape	0.257 **		0.884 ***	0.965 ***	0.730 ***	0.897 ***	0.877 ***	0.841 ***	-0.798 ***	0.472 ***	0.423 ***	0.332 ***	0.400 ***
3: Total class Area	0.557 ***	0.884 ***		0.845 ***	0.922 ***	0.762 ***	0.844 ***	0.776 ***	-0.753 ***	0.380 ***	0.365 ***	0.249 **	0.341 ***
4: Percentage of open Landscape	0.280 ***	0.965 ***	0.845 ***		0.684 ***	0.827 ***	0.817 ***	0.777 ***	-0.769 ***	0.326 ***	0.335 ***	0.173 *	0.323 ***
5: Total Edge	0.766 ***	0.730 ***	0.922 ***	0.684 ***		0.541 ***	0.667 ***	0.574 ***	-0.706 ***	0.335 ***	0.429 ***	0.195 *	0.393 ***
6: Patch Area - Mean	-0.042	0.897 ***	0.762 ***	0.827 ***	0.541 ***		0.863 ***	0.852 ***	-0.633 ***	0.598 ***	0.275 **	0.464 ***	0.218 *
7: Total Core Area	0.195 *	0.877 ***	0.844 ***	0.817 ***	0.667 ***	0.863 ***		0.981 ***	-0.662 ***	0.499 ***	0.363 ***	0.347 ***	0.311 ***
8: Percent core area	0.107	0.841 ***	0.776 ***	0.777 ***	0.574 ***	0.852 ***	0.981 ***		-0.608 ***	0.485 ***	0.357 ***	0.332 ***	0.302 ***
9: Euclidean Nearest Neighbor Distance - Mean	-0.387 ***	-0.798 ***	-0.753 ***	-0.769 ***	-0.706 ***	-0.633 ***	-0.662 ***	-0.608 ***		-0.409 ***	-0.398 ***	-0.300 ***	-0.396 ***
10: Landscape continuity in maquis and forest	-0.181 *	0.472 ***	0.380 ***	0.326 ***	0.335 ***	0.598 ***	0.499 ***	0.485 ***	-0.409 ***		0.323 ***	0.905 ***	0.250 **
11: Connectivity of the landscape in maquis and forest	0.260 **	0.423 ***	0.365 ***	0.335 ***	0.429 ***	0.275 **	0.363 ***	0.357 ***	-0.398 ***	0.323 ***		0.260 **	0.927 ***
12: Landscape continuity – overall	-0.259 **	0.332 ***	0.249 **	0.173 *	0.195 *	0.464 ***	0.347 ***	0.332 ***	-0.300 ***	0.905 ***	0.260 **		0.258 **
13: Connectivity of the landscape - overall	0.267 **	0.400 ***	0.341 ***	0.323 ***	0.393 ***	0.218 *	0.311 ***	0.302 ***	-0.396 ***	0.250 **	0.927 ***	0.258 **	

Table 6: Correlation matrix of different fragmentation metrics for the agricultural areas, calculated for the 46 sections over the three time periods, within a buffer of 8 km around Highway 6 (n = 138). * p < 0.05, ** p < 0.01, *** p < 0.001.

	1	2	3	4	5	6	7	8	9	10	11	12	13
1: Number of patches		-0.318 ***	0.516 ***	-0.152	0.633 ***	-0.558 ***	0.014	-0.369 ***	-0.312 ***	-0.446 ***	0.196 *	-0.371 ***	0.114
2: Percent of total landscape	-0.318 ***		0.464 ***	0.812 ***	-0.114	0.852 ***	0.724 ***	0.764 ***	-0.606 ***	0.339 ***	0.040	0.129	-0.206 *
3: Total class Area	0.516 ***	0.464 ***		0.388 ***	0.611 ***	0.364 ***	0.812 ***	0.453 ***	-0.554 ***	0.056	0.159	-0.061	-0.057
4: Percentage of open Landscape	-0.152	0.812 ***	0.388 ***		-0.378 ***	0.597 ***	0.598 ***	0.635 ***	-0.672 ***	-0.133	-0.082	-0.349 ***	-0.437 ***
5: Total Edge	0.633 ***	-0.114	0.611 ***	-0.378 ***		-0.125	0.230 **	-0.112	-0.110	0.244 **	0.245 **	0.297 ***	0.307 ***
6: Patch Area - Mean	-0.558 ***	0.852 ***	0.364 ***	0.597 ***	-0.125		0.735 ***	0.841 ***	-0.240 **	0.539 ***	-0.085	0.333 ***	-0.225 **
7: Total Core Area	0.014	0.724 ***	0.812 ***	0.598 ***	0.230 **	0.735 ***		0.862 ***	-0.421 ***	0.296 ***	-0.081	0.085	-0.306 ***
8: Percent core area	-0.369 ***	0.764 ***	0.453 ***	0.635 ***	-0.112	0.841 ***	0.862 ***		-0.231 **	0.409 ***	-0.232 **	0.176 *	-0.423 ***
9: Euclidean Nearest Neighbor Distance - Mean	-0.312 ***	-0.606 ***	-0.554 ***	-0.672 ***	-0.110	-0.240 **	-0.421 ***	-0.231 **		0.182 *	-0.245 **	0.253 **	0.018
10: Landscape continuity in agricultural areas	-0.446 ***	0.339 ***	0.056	-0.133	0.244 **	0.539 ***	0.296 ***	0.409 ***	0.182 *		0.008	0.926 ***	0.122
11: Connectivity of the landscape in agricultural areas	0.196 *	0.040	0.159	-0.082	0.245 **	-0.085	-0.081	-0.232 **	-0.245 **	0.008		0.038	0.863 ***
12: Landscape continuity – overall	-0.371 ***	0.129	-0.061	-0.349 ***	0.297 ***	0.333 ***	0.085	0.176 *	0.253 **	0.926 ***	0.038		0.258 **
13: Connectivity of the landscape - overall	0.114	-0.206 *	-0.057	-0.437 ***	0.307 ***	-0.225 **	-0.306 ***	-0.423 ***	0.018	0.122	0.863 ***	0.258 **	

DISCUSSION

Changes in land cover

We found that with greater proximity to Highway 6, the higher and faster were the changes in the extent of the development of built areas. Furthermore, the changes in the extent of built-up areas near the road was greater following the construction of new road sections. These processes are consistent with known impacts of road infrastructure leading to decreases in natural land cover classes and open areas (Fearnside, 2015; Walker *et al*., 2013).

Habitat fragmentation

We found a greater decrease in the coverage of the open landscape classes within a distance of 1 km from Highway 6 than within the 0-8 km range. The decrease that occurred in the range 0-1 km from the road was relatively larger and more extensive. This decrease was found for all three classes of open landscape areas (and especially for agricultural areas; Table 3), both for the total area of each habitat, and for the total core areas of these habitats. The core area represents the less disturbed area of the habitat; when road networks pass through habitats areas, they will reduce the extent and possibly also the quality of the core area, converting what previously was interior habitat into edge habitat and reducing its ability to prevent marginal disturbance in the habitat (Dramstad *et al*., 1996; Reed *et al*., 1996). The decrease in core areas is a clear indication of the fragmentation process taking place (Dramstad *et al*., 1996; Reed *et al*., 1996; Tinker, 1998).

We found a strong correlation (for the three habitat classes) between the decrease of percentage of landscape of the habitats and the increase in the average distance between the patches of the habitats (Euclidean Nearest Neighbor Distance). This increase in the distance between neighboring patches means increased isolation of the habitat, again emphasizing the fragmentation of the landscape following the construction of Highway 6 (Haig *et al*., 2000). The correlations between the fragmentation metrics were weaker for the agricultural habitat patches than for the Mediterranean maquis and planted forests as well as for the batha and shrubland areas (Tables 4-6). This is probably explained by the greater coverage of agricultural areas (and hence their smaller fragmentation before road construction started; Table 3, Fig. 5) in comparison with the two other classes of open areas.

Examination of the various landscape metrics which were analyzed using the landscape structure program Fragstats, allowed us to quantify the differences in complexity and variability of the fragmentation metrics that changed due to the removal of habitat areas. In relation to the other approaches, the indicators tested in Fragstats examined changes created by highway 6 at the individual level of different habitat patches (e.g. the changes in the number of the patchers, the core area or the patches' edges). Using this approach, we showed the changes in the patches that make up each habitat, unlike the other analyzes that applied a continuous approach, without any a-priori mapping of habitat classes (Bruton *et al*., 2015).

Changes in landscape continuity

We found that the greatest changes in landscape continuity between the years 1997 and 2019 took place within 1 km from Highway 6. The various environmental impacts of roads on their surrounding areas include light and noise pollution, heavy metals, particulate matters and NO_2, and often follow exponential distance decay functions (Phillips *et al*., 2021). This decay function resembles our finding that the greatest changes in landscape continuity were in proximity to Highway 6.

These findings are consistent with the impacts related to construction of roads, which also decrease with distance from roads, with correlations found between the distance from the road and landscape pattern changes (Benítez-López *et al*., 2010; Grade & Sieving, 2016; Liu *et al*., 2014; Reeves *et al*., 2008; Santos & Tabarelli, 2002; Slabbekoorn, 2019; Reisner & Malkinson, 2019).

The changes in landscape continuity which we quantified, were most pronounced in the buffer areas (i.e. termed here as Sections) surrounding recently built stretches of the highway, and not in other areas, indicating that decrease in landscape continuity was associated with the new highway, and not a result of overall development of built-up areas. These results indicate that the processes of disruption and damage on a higher and faster scale, occurred in accordance with the time periods in which highway 6 was paved. Just as road infrastructure may cause damage to natural and open areas and lead to disruption and fragmentation of the landscape continuity (Forman & Alexander, 1998; Liu *et al*., 2014; Shirvani *et al.*, 2020), it can be concluded that highway construction was the main driver for significant changes in landscape continuity in the studied area (Roedenbeck *et al*., 2007).The added value of the landscape continuity approach is that it does not assume any natural core-areas compared to methods of ecological networks and does not require an a-priori segmentation of the study area into habitat patches. Instead, it allowed us to define quantitative values for each grid cell, based on its weighted distance from the different types of the built-up areas (and their possible influence on the landscape continuity). The dimension of fragmentation measured by this approach is not dependent on the type of natural habitat but rather on its size, with higher values within 'core' areas; in addition, this type of analysis is affected on estimates of the potential impact of different types of built-up areas (Levin *et al*., 2007). In order to reduce the negative impacts of roads and new neighborhoods on landscape continuity, it has been recommended to favor new development projects to be adjacent to existing ones (Levin *et al*., 2007).

Changes in the connectivity of the heterogeneous landscape

As with the previous metrics we found that larger changes in the connectivity of the heterogeneous landscape (i.e., the enhancement of bottlenecks) took place in the area closer to the highway route. We found statistically significant changes for the group of road sections which were built between 1999-2009 – these road sections were built in the center of Israel (Fig. 1) – which is also the more densely populated area, where landscape connectivity and the availability of open spaces were lower even before Highway 6 was built (Levin *et al*., 2007). Moreover, we found that as the distance from the Highway increased, the effect of the highway construction gradually decreased and became smaller and was no longer found to be statistically significant. These results are consistent with the claim that the construction of roads is related to damage and changes that occur in the surrounding environment, when there is a connection between the distance measured from the road and the intensity of damage measured in the environment (Benítez-López *et al*., 2010; Grade & Sieving, 2016; Liu *et al*., 2014; Reeves *et al*., 2008; Santos & Tabarelli, 2002; Slabbekoorn, 2019; Reisner & Malkinson, 2019). These findings are consistent with the fact that construction of roads causes the fragmentation and loss of habitats, and that roads lead to changes in the natural land cover classes, causing the formation of barriers, thus disrupting the natural pattern of the landscape and interrupting the continuity and connectivity of landscape (Fu *et al*., 2010; Laurance *et al*., 2009; Poessel *et al.*, 2014).

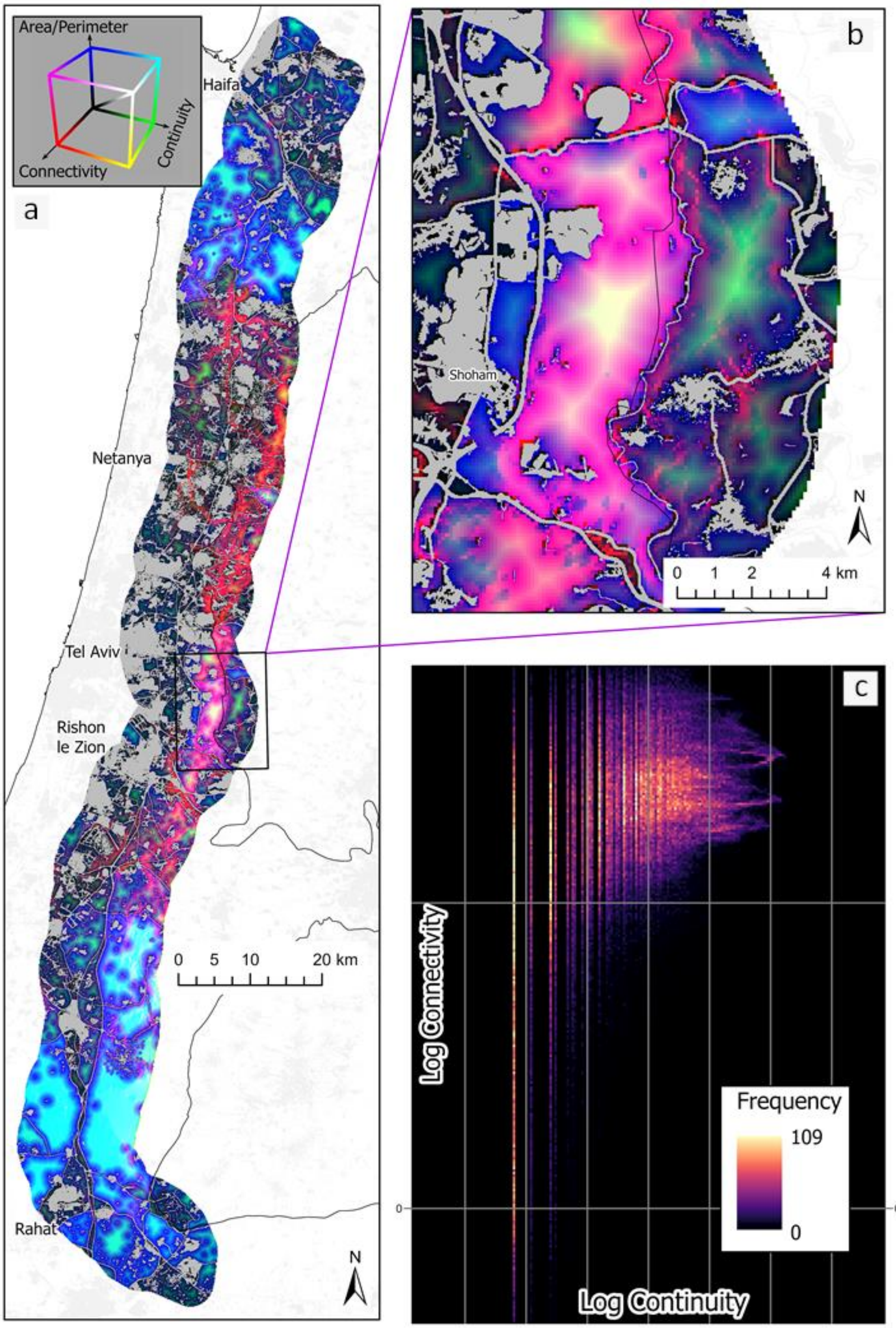
The fragmentation aspect that is expressed in this approach, provides an ecological interpretation of the potential movement wildlife through this changing landscape (which was affected by the fragmentation process). The circuit model approach estimates the net movement probabilities (or flow) of random walkers via any grid cell (McRae *et al*., 2008), thus expressing the connectivity and the changing of transmission capacity (animals movement ability), based on possible models of spatial connectivity. This approach especially emphasizes critical areas for the movement of wildlife, and elements such as narrow corridors, barriers and bottlenecks that were created or disappeared as a result of the construction of highway 6.

Comparison between the different approaches for quantifying landscape fragmentation, continuity, and connectivity

While some of the patch-based fragmentation metrics derived from Fragstats were highly correlated between themselves (as reported previously by Hargis *et al.*, 1998), the correlations between most of those fragmentation metrics with the continuity and connectivity metrics were quite low. These results, emphasize the complementarity of assessing the impact of land cover changes and road construction using several metrics, and not to focus on a single metric. Previous studies that compared fragmentation metrics often focused on patch-based metrics for a single time frame (Fan & Myint, 2014; Sánchez-Fernández *et al.*, 2022), or used simulations to understand the behavior of patch-based fragmentation metrics (Hargis *et al.*, 1998; Wang *et al.*, 2014). The combined use of landscape metrics and connectivity analysis over time, as done here, has been recommended to assist planners in understanding the impacts of land cover changes on ecological connectivity (Almenar *et al*., 2019). The advantage of continuous metrics such as connectivity derived from Circuitscape or landscape continuity, is that they are not relying on the mapping of habitat classes which can vary greatly based on the land cover classes used and the way the classification is done. In addition, continuous metrics provide us with pixel-based maps which enable a more holistic view of the study area, and allow to also derive maps mapping changes in landscape continuity or connectivity, and to spatially identify where changes have been greatest. However, the approaches used to map landscape continuity or connectivity also rely on partly arbitrary definitions, such as the weights assigned to different built-up area classes or the cost distance weights assigned to different land cover classes.

The differences between the three approaches for mapping landscape fragmentation can be visualized when overlapping them. Fig.12 presents a false color composite of the landscape connectivity (in red), landscape continuity (in green), and one of the derived patch-based metrics, the area/perimeter ratio (in blue, as of 2019). Had all metrics been the same, the map would have been only in shades of grey. However, this is not the case. The central sections of highway 6, where landscape continuity was low, were consequently highlighted as critical areas for landscape connectivity (given that wildlife will have less free movement options), and are mostly colored in red hues (Fig. 12a). In the southern and northern sections of highway 6, open landscape habitats are larger in size (i.e. a higher area/perimeter ratio) and landscape continuity is higher, hence many areas are colored in cyan, indicating high landscape continuity and a high area/perimeter ratio (hence, low edge effects). However, the area/perimeter ratios are uniform within a habitat patch (as they are calculated at the polygon level), and therefore this approach is not suited to a grid cell representation as it is based on a-priori mapping of habitat patches. Note the blue hues at the edges of many natural patches, where landscape continuity values are low (Fig. 12a). In most cases, where landscape continuity was high, the connectivity value was low (Fig. 12c). High values of landscape connectivity (indicating bottlenecks and critical areas for wildlife movement) were mostly found between low and medium values of landscape continuity (Fig. 12c).

Fig. 12: (a) False color composite of the 2019 layers of landscape connectivity (in red), landscape continuity (in green) and the area/perimeter ratio (in blue). (b) Zoom-in of the map shown in a. (c) Scatter plot showing the correspondence between Log continuity and Log connectivity. The grey areas in a and b represent built-up areas, roads, and other built-up structures.



Hence the landscape continuity approach provides us with a proxy for core natural areas where the estimated impact of built-up areas will be low, whereas the landscape connectivity approach provides us with a proxy for critical areas for the movement of wildlife between such core areas. Where landscape continuity is very high, landscape connectivity would usually not be high, because such areas would usually not be critical areas for wildlife movement. Only in one location (east of the new town of Shoham), nestled tightly between highway 6 and the separation wall, were all three metrics high (see the white area at the center of Fig. 12b). Using these different analysis approaches, it became possible to process and to display different fragmentation scales, with differing strengths and different contexts regarding the process that took place in the landscape. Moreover, both continuous approaches can be used to evaluate and visualize the future impact of development plans, and to examine which development scenarios will have fewer negative impacts of landscape fragmentation.

CONCLUSIONS

In this study we examined the impact of the construction of a major highway over twenty years on changes in a wide range of landscape metrics: both patch-based metrics and continuous metrics. All approaches identified that landscape fragmentation processes were most acute within 1 km from the newly built highway. Our analysis also demonstrated that these different approaches for quantifying landscape fragmentation, continuity and connectivity are complementary, and all contribute to our understanding of landscape changes.

CONFLICTS OF INTEREST

The authors declare no conflict of interest.

REFERENCES

Almenar, J. B., Bolowich, A., Elliot, T., Geneletti, D., Sonnemann, G., & Rugani, B. (2019). Assessing habitat loss, fragmentation and ecological connectivity in Luxembourg to support spatial planning. *Landscape and Urban Planning*, 189, 335-351.

Angold, P. G. (1997). The impact of a road upon adjacent heathland vegetation: effects on plant species composition. *Journal of Applied Ecology*, 34(2), 409-417.

Ahiron-Fromkin, T. (ed.). (2012). *Habitat Fragmentation by Transportation Infrastructure: A Guide to Identifying Conflicts and Planning Solutions*. The National Road Company. Israel.

Benítez-López, A., Alkemade, R., & Verweij, P. A. (2010). The impacts of roads and other infrastructure on mammal and bird populations: a meta-analysis. *Biological conservation*, 143(6), 1307-1316.

Bruschi, D., Garcia, D. A., Gugliermetti, F., & Cumo, F. (2015). Characterizing the fragmentation level of Italian's National Parks due to transportation infrastructures. *Transportation Research Part D: Transport and Environment*, 36, 18-28.

Bruton, M. J., Maron, M., Levin, N., & McAlpine, C. A. (2015). Testing the relevance of binary, mosaic and continuous landscape conceptualisations to reptiles in regenerating dryland landscapes. *Landscape Ecology*, 30, 715-728.

Brooks, T. M., Mittermeier, R. A., Mittermeier, C. G., Da Fonseca, G. A., Rylands, A. B., Konstant, W. R., ... & Hilton‐Taylor, C. (2002). Habitat loss and extinction in the hotspots of biodiversity. *Conservation biology,* 16(4), 909-923.

Costanza, R., d'Arge, R., De Groot, R., Farber, S., Grasso, M., Hannon, B., ... & Van Den Belt, M. (1997). The value of the world's ecosystem services and natural capital. *Nature,* 387 (6630), 253-260.

Denneboom, D., Bar-Massada, A., & Shwartz, A. (2021). Factors affecting usage of crossing structures by wildlife–A systematic review and meta-analysis. *Science of the Total Environment*, *777*, 146061.

Detwyler, T.R. (1971). *Man's Impact on Environment***.** McGraw-Hill, London.

Dickson, B. G., Albano, C. M., Anantharaman, R., Beier, P., Fargione, J., Graves, T. A., ... & Theobald, D. M. (2019). Circuit‐theory applications to connectivity science and conservation. *Conservation Biology*, 33(2), 239-249.

Dramstad, W. E., Olson, J. D., & Forman, R. T. (1996). *Landscape ecology principles in landscape architecture and land-use planning.* Harvard University Graduate School of Design.

Fahrig, L. (1997). Relative effects of habitat loss and fragmentation on population extinction. *The Journal of Wildlife Management*, 61(3), 603-610.

Fahrig, L. (2003). Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, 487-515.

Fan, C., & Myint, S. (2014). A comparison of spatial autocorrelation indices and landscape metrics in measuring urban landscape fragmentation. *Landscape and Urban Planning*, 121, 117-128.

Fearnside, P. M. (2015). Highway construction as a force in destruction of the Amazon Forest. *Handbook of road ecology***,** 414-424.

Forman, R.T. & Alexander, L.E. (1998). Roads and their major ecological effects. *Annual Review of Ecology and Systematic,* 29**,** 207-231.

Forman, R. T., Sperling, D., Bissonette, J. A., Clevenger, A. P., Cutshall, C. D., Dale, V. H., ... & Winter, T. C. (2003). *Road ecology: science and solutions***.** Island press.

Fu, W., Liu, S., Degloria, S. D., Dong, S., & Beazley, R. (2010). Characterizing the "fragmentation–barrier" effect of road networks on landscape connectivity: A case study in Xishuangbanna, Southwest China. *Landscape and urban planning*, 95(3), 122-129.

Geneletti, D. (2003). Biodiversity impact assessment of roads: an approach based on ecosystem rarity. *Environmental Impact Assessment Review,* 23(3), 343-365.

Geneletti, D. (2006). Some common shortcomings in the treatment of impacts of linear infrastructures on natural habitat. *Environmental Impact Assessment Review,* 26(3), 257-267.

Gerlach, G., & Musolf, K. (2000). Fragmentation of landscape as a cause for genetic subdivision in bank voles. *Conservation biology,* 14(4), 1066-1074.

Grade, A. M., & Sieving, K. E. (2016). When the birds go unheard: highway noise disrupts information transfer between bird species. *Biology Letters,* 12(4), 20160113.

Haddad, N. M., Brudvig, L. A., Clobert, J., Davies, K. F., Gonzalez, A., Holt, R. D., ... & Cook, W. M. (2015). Habitat fragmentation and its lasting impact on Earth's ecosystems. *Science Advances,* 1(2), e1500052.

Hawbaker, T. J., Radeloff, V. C., Clayton, M. K., Hammer, R. B., & Gonzalez-Abraham, C. E. (2006). Road development, housing growth, and landscape fragmentation in northern Wisconsin: 1937–1999. *Ecological Applications*, 16(3), 1222-1237.

Haig, A. R., Matthes, U., & Larson, D. W. (2000). Effects of natural habitat fragmentation on the species richness, diversity, and composition of cliff vegetation**.** *Canadian journal of botany,* 78(6), 786-797.

Hargis, C. D., Bissonette, J. A., & David, J. L. (1998). The behavior of landscape metrics commonly used in the study of habitat fragmentation. *Landscape Ecology,* 13, 167-186.

Harrington, G. N., & Sanderson, K. (1994). Recent contraction of wet sclerophyll forest in the wet tropics of Queensland due to invasion by rainforest. *Pacific Conservation Biology,* 1(4), 319-327.

Heilman, G. E., Strittholt, J. R., Slosser, N. C., & Dellasala, D. A. (2002). Forest Fragmentation of the Conterminous United States: Assessing Forest Intactness through Road Density and Spatial Characteristics: Forest fragmentation can be measured and monitored in a powerful new way by combining remote sensing, geographic information systems, and analytical software. *BioScience*, 52(5), 411-422.

Karlson, M., & Mörtberg, U. (2015). A spatial ecological assessment of fragmentation and disturbance effects of the Swedish road network. *Landscape and Urban Planning*, 134, 53-65.

Kaplan, M., & Slotsky, M. (2002). A methodology for assessing the value and sensitivity of the open landscape. *Essays in the Management of Natural and Environmental Resources,* 2, 59-79.

Konstantopoulos, K., Moustakas, A., & Vogiatzakis, I. N. (2020). A spatially explicit impact assessment of road characteristics, road-induced fragmentation and noise on birds species in Cyprus. *Biodiversity*, 21(1), 61-71.

Kupfer, J. A. (2012). Landscape ecology and biogeography: rethinking landscape metrics in a post-FRAGSTATS landscape. *Progress in Physical Geography*, 36(3), 400-420.

Laforge, A., Barbaro, L., Bas, Y., Calatayud, F., Ladet, S., Sirami, C., & Archaux, F. (2022). Road density and forest fragmentation shape bat communities in temperate mosaic landscapes. *Landscape and Urban Planning,* 221, 104353.

Laurance, W. F., Goosem, M., & Laurance, S. G. (2009). Impacts of roads and linear clearings on tropical forests. *Trends in Ecology & Evolution*, 24(12), Pp 659-669.

Levin, N., Lahav, H., Ramon, U., Heller, A., Nizry, G., Tsoar, A., & Sagi, Y. (2007). Landscape continuity analysis: A new approach to conservation planning in Israel. *Landscape and Urban Planning,* 79*(*1), 53-64.

Lindenmayer, D. B., & Fischer, J. (2013). *Habitat fragmentation and landscape change: an ecological and conservation synthesis***.** Island Press.

Liu, S., Dong, Y., Deng, L., Liu, Q., Zhao, H., & Dong, S. (2014). Forest fragmentation and landscape connectivity change associated with road network extension and city expansion: A case study in the Lancang River Valley. *Ecological indicators,* 36, 160-168.

Longcore, T., & Rich, C. (2004). Ecological light pollution. *Frontiers in Ecology and the Environment*, 2(4), 191-198.

McGarigal, K. (1995). *FRAGSTATS: spatial pattern analysis program for quantifying* *landscape structure* (Vol. 351). US Department of Agriculture, Forest Service, Pacific Northwest Research Station.

McRae, B. H., Dickson, B. G., Keitt, T. H., & Shah, V. B. (2008). Using circuit theory to model connectivity in ecology, evolution, and conservation. *Ecology*, 89(10), 2712-2724.

McRae, B. H., Shah, V. B., & Mohapatra, T. K. (2009). Circuitscape user’s guide. *The University of California, Santa Barbara*.

McRae, B. H., Shah, V., & Edelman, A. (2016). Circuitscape: modeling landscape connectivity to promote conservation and human health. *The Nature Conservancy*, 14, 1-14.

Phillips, B. B., Bullock, J. M., continOsborne, J. L., & Gaston, K. J. (2021). Spatial extent of road pollution: A national analysis. *Science of the Total Environment*, 773, 145589.

Poessel, S. A., Burdett, C. L., Boydston, E. E., Lyren, L. M., Alonso, R. S., Fisher, R. N., & Crooks, K. R. (2014). Roads influence movement and home ranges of a fragmentation-sensitive carnivore, the bobcat, in an urban landscape. *Biological Conservation*, 180, 224-232.

Rayfield, B., Fortin, M. J., & Fall, A. (2011). Connectivity for conservation: a framework to classify network measures. *Ecology*, 92*(*4), 847-858.

Reed, R. A., Johnson-Barnard, J., & Baker, W. L. (1996). Contribution of roads to forest fragmentation in the Rocky Mountains. *Conservation Biology*, 10(4), 1098-1106.

Reeves, M. K., Dolph, C. L., Zimmer, H., Tjeerdema, R. S., & Trust, K. A. (2008). Road proximity increases risk of skeletal abnormalities in wood frogs from National Wildlife Refuges in Alaska. *Environmental Health Perspectives*, 116(8), 1009-1014.

Reisner, Y., & Malkinson, D. (2019). The Impact of Roads on Wildlife Activity in a Fragmented Habitat. *Horizons in Geography*, 95, 117-127.

Roedenbeck, I. A., Fahrig, L., Findlay, C. S., Houlahan, J. E., Jaeger, J. A., Klar, N., Van der Grift, E. A. (2007). The Rauischholzhausen agenda for road ecology. *Ecology and Society*, 12(1).

Sánchez-Fernández, M., Barrigón Morillas, J. M., Montes González, D., & de Sanjosé Blasco, J. J. (2022). Impact of roads on environmental protected areas: analysis and comparison of metrics for assessing habitat fragmentation. *Land*, 11(10), 1843.

Santos, A. M., & Tabarelli, M. (2002). Distance from roads and cities as a predictor of habitat loss and fragmentation in the caatinga vegetation of Brazil. *Brazilian Journal of Biology*, 62, 897-905.

Saunders, D. A., Hobbs, R. J., & Margules, C. R. (1991). Biological consequences of ecosystem fragmentation: a review. *Conservation Biology*, 5(1), 18-32.

Schaffer, G., & Levin, N. (2014). Mapping Human Induced Landscape Changes in Israel Between the end of the 19 Century and the Beginning of the 21 Century. *Journal of Landscape Ecology*, 7(1), 110-145.

Shirvani, Z., Abdi, O., & Buchroithner, M. F. (2020). A new analysis approach for long-term variations of forest loss, fragmentation, and degradation resulting from road-network expansion using Landsat time-series and object-based image analysis. *Land Degradation & Development*, 31(12), 1462-1481.

Slabbekoorn, H. (2019). Noise pollution. *Current Biology*, 29 (19), R957-R960.

Smith, E. P., Orvos, D. R., & Cairns Jr, J. (1993). Impact assessment using the before-after-control-impact (BACI) model: concerns and comments. *Canadian Journal of Fisheries and Aquatic Sciences*, 50*(*3), 627-637.

Song, J., Ye, J., Zhu, E., Deng, J., & Wang, K. (2016). Analyzing the impact of highways associated with farmland loss under rapid urbanization. *ISPRS International Journal of Geo-Information,* 5(6)*,* 94.

Spellerberg, I. F. (2002). *Ecological Effects of Roads: The Land Reconstruction and Management.* CRC Press.

Tinker, D. B., Resor, C. A., Beauvais, G. P., Kipfmueller, K. F., Fernandes, C. I., & Baker, W. L. (1998). Watershed analysis of forest fragmentation by clearcuts and roads in a Wyoming forest. *Landscape ecology*, 13, 149-165.

Tsunokawa, K., & Hoban, C. (1997). *Roads and the environment: a handbook.*

Trombulak, S. C., & Frissell, C. A. (2000). Review of ecological effects of roads on terrestrial and aquatic communities. *Conservation Biology,* 14*(*1), 18-30.

Vos, C. C., & Opdam, P. (Eds.). (1993). *Landscape ecology of a stressed environment***.** London: Chapman & Hall.

Walker, R., Arima, E., Messina, J., Soares-Filho, B., Perz, S., Vergara, D., ... & Castro, W. (2013). Modeling spatial decisions with graph theory: logging roads and forest fragmentation in the Brazilian Amazon. *Ecological applications,* 23*(*1), 239-254.

Wang, X., Blanchet, F. G., & Koper, N. (2014). Measuring habitat fragmentation: An evaluation of landscape pattern metrics. *Methods in Ecology and Evolution,* 5(7), 634-646.

Wilcove, D. S. (1986). Habitat fragmentation in the temperatezone. *Conservation biology*, 237-256.

Zohar, I., Bookman, R., Levin, N., De Stigter, H., & Teutsch, N. (2014). Contamination history of lead and other trace metals reconstructed from an urban winter pond in the eastern Mediterranean Coast (Israel). *Environmental Science & Technology,* 48(23), 13592-13600.

Yom-Tov, Y., Balaban, A., Hadad, E., Weil, G., & Roll, U. (2020). The plight of the Endangered Mountain gazelle Gazella gazella. *Oryx***,** 1-8.

Website: - Highway 6 information site- *www.kvish6.co.il.*

- Hamaarag, the national program for assessing the state of nature in Israel- *www.hamaarag.org.il*

- Information website of the Ministry of Agriculture in Israel – *data1-moag.opendata.arcgis.com*

- The government site for maps of Israel- *govmap.gov.il*

- Information website of the Ministry of Transportation in Israel- *geo.mot.gov.il*

- Open street map, the free wiki world map- *openstreetmap.org*

SUPPLEMENTS

Fig. S1: Division of the research area according to the land categories

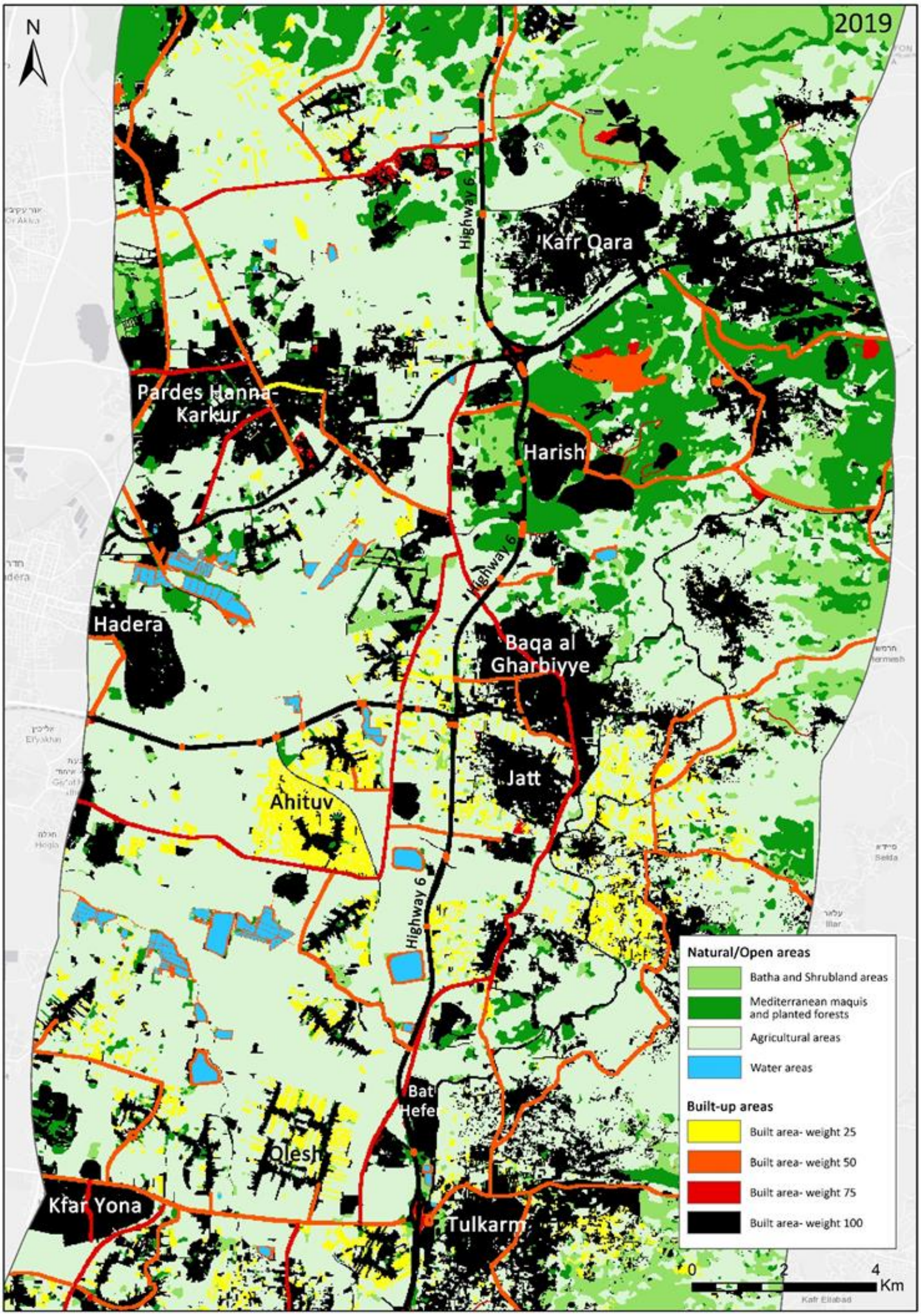


Fig. S2: The development of the built-up area in the study area throughout the years 1997-2019 – Zoom in maps of two areas included in the map shown in Fig. 3.

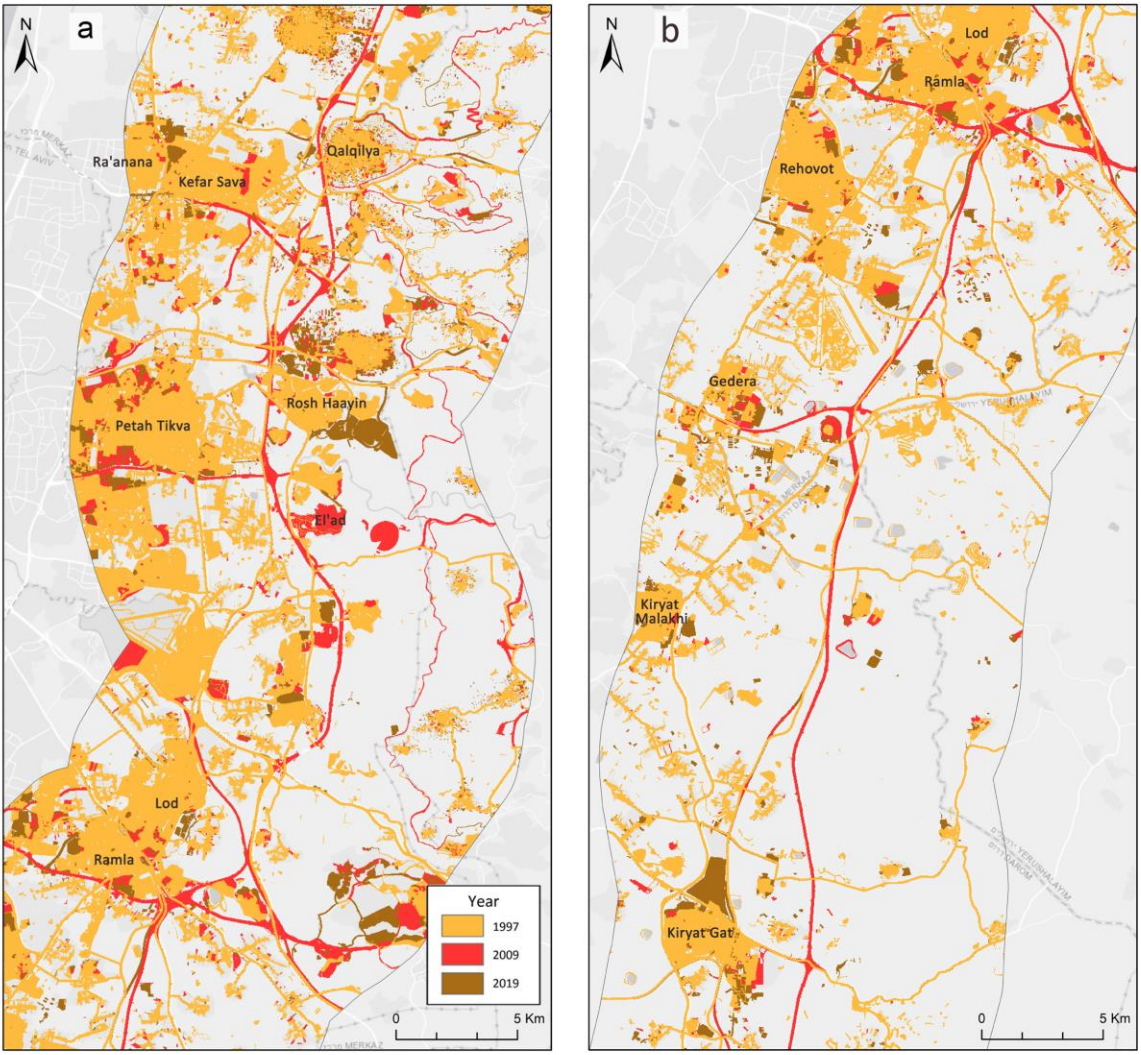
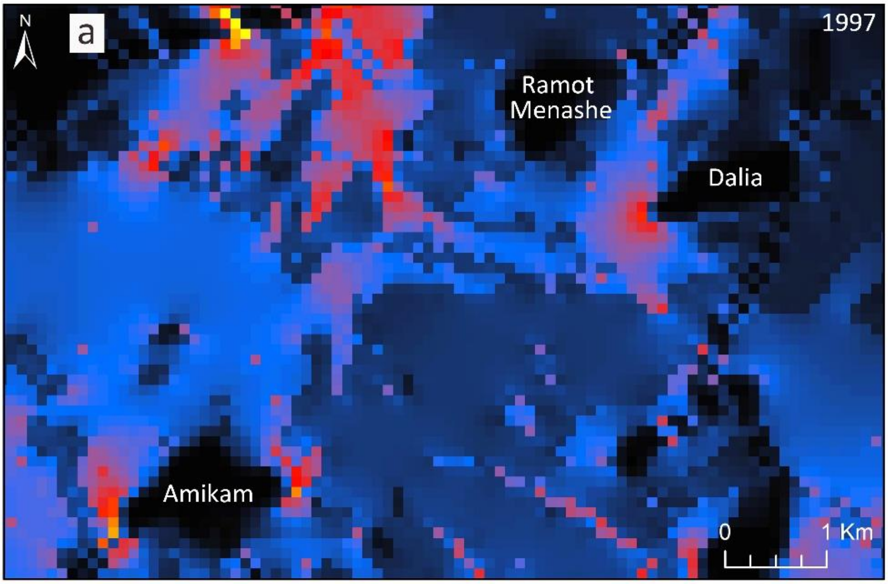


Fig. S3: Landscape connectivity values derived from Circuitscape in the area of the 'Dalia' ecological overpass, in the years 1997 and 2019



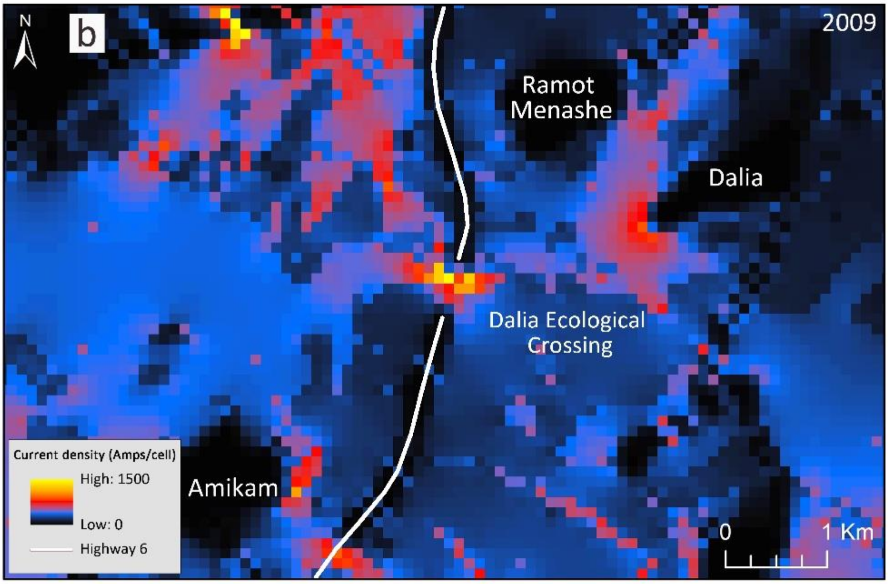


Table S1: Schedule of the Highway 6 sections construction

Section	Section Name	Section Length (km)	The time when the construction of the section started	The time the section opened	Structures in the section
1	Somech- Sha'ar HaAmakim	10.5	Northern part - was exist as highway 70; Adding a lane and building a Somech interchange in 2011 (previously existed as a T junction) 2015- Southern part (the 2 tunnels in the section)	2011- upgrading of the road and the construction of the Somech interchange 2019- Southern part	Ibtin tunnel Rekhasim tunnel
2	Sha'ar HaAmakim- Tel Qashish	5.5	2015- Northern part Southern part - was exist as highway 70; upgraded in 2013	2018- Partial opening 2019- Full opening	
3	Tel Qashish- Eliakim	5	2016- Northern part (tunnel part) Southern part – was exist as Highway 70; The road upgrade from 2016	2018	Yokneam tunnel
4	Eliakim- Ein Tut	5	Middle part - highway 70 2005- Southern part and upgrading the northern part	2009	
5	Ein Tut- Iron	18	2004	2009	Dalia tunnel (ecological crossing) Nili tunnel

6	Iron- Baqa Jatt	5	2003 (2012- Another lane)	2004 (2014- Another lane)	
7	Baqa Jatt- Nitzanei Oz	11	2003 (2012- Another lane)	2004 (2014- Another lane)	
8	Nitzanei Oz- Eyal	13	2001	2003	
9	Eyal- Horshim	8	1999	2002	
10	Horshim- Qesem	3	1999	2002	
11	Qesem- Nahshonim	5	1999	2002	
12	Nahshonim- Ben Shemen	15	1999	2002	Hadid tunnel
13	Ben Shemen- Daniel	4	2001	2003	
14	Daniel- Nesharim	4	2001	2003	
15	Nesharim- Sorek	14	2001	2003	
16	Sorek- Kiryat Gat	23	2004	2007	
17	Kiryat Gat- Ma’ahaz	12	2005	2008	
18	Ma’ahaz- Kama	6	Middle part – was exist as Highway 40; Upgrade from 2014 2014- Southern and northern part - construction	2015	

19	Kama- Dvira	4	2014- Northern part- Southern part- Highway 40; Upgrade and construction of the interchanges from 2014	2015- Northern part (Kama Interchange)- 2016- Southern part (Dvira Interchange)	
20	Dvira- Rahat	2.5	(Part of the section is Highway 40) 2014- The other part - building the interchanges, upgrading the road, and building a lane	2018	
21	Rahat- Lehavim	3	2013	2016	
22	Lehavim- Lakiya	6.8	2013- Northern part and southern part - Middle part - Highway 31, upgrade of the part from 2013	2016	
23	Lakiya- Shoket	7.4	2014	2016	

Table S2: Construction of lateral roads built as part of the Highway 6 project

Road Number	Road Name	Road Length (km)	The time when the construction of the road started	The time the road opened
77	From Tel Qashish interchange to Yishai interchange	6	2018	2019
9	From Baqa-Jatt interchange to Highway 4	10.2	2010 (The eastern part marked as Road 61 paved in 2005)	2014
531	From Horshim interchange to Shmaryahu-east interchange	14	2008	2018
471	From Nahshonim interchange to Bar-Ilan interchange	9.5	1999	2003- the eastern part (near the Nahshonim interchange) 2008- most parts of the road 2012- The part of the road between the Gat Rimon-Shaaria (Petah Tikva) interchanges 2013- Completion of the entire road (interchanges and upgrading)
431	From Nesharim interchange to Mevo-Ayalon interchange	15.7	2005	2008- in the western part- Mevo-Ayalon Interchange, Kiryat-Rishon Interchange,

				Rishon-South Interchange 2009- in the eastern part- connecting to Highway 6 via Nesharim Interchange, towards Anava Interchange on Highway 1, until Modi'in-Maccabim-Reot
7	From Sorek interchange to Gedera interchange	7.4	2001	2004- Partial opening 2014- Final after another upgrade (Upgrading the western part and replacing road 41)
293	From Kama interchange to Beit-Kama (extension of road 293 from Beit Kama junction to the intersection with Highway 6 at Kama interchange)	1	2014	2015

Table S3: Existing GIS layers which we used to map land cover for the year 2019

data name	data source
The Israel land cover	"Hamaarag"- The National Program for Assessing the state of nature in Israel (hamaarag.org.il)
Agricultural lands	Government Ministry of Agriculture website (data1-moag.opendata.arcgis.com)
Areas of industrial facilities	Government Ministry of Transportation website (geo.mot.gov.il)
Israel's roads, dirt roads, the railway line, and the separation-wall	The Center for Computational Geography (The Hebrew University of Jerusalem), and Open Street Map (openstreetmap.org)

Table S4: Data sources used to reconstruct land cover for the years 1997, 2009 and 2019

data name	data source
Orthophoto Israel of 1997, 2009, 2019	Israel's government map site, the Israel Mapping Center (govmap.gov.il)
Landsat satellite images (annual)	landsat.gsfc.nasa.gov, and earthengine.google.com/timelapse
Topographic maps 1:50,000 of the 1990s	The Israel Mapping Center (Levy et al., 2015)
Road atlas 1998	Melzer, M. (1998). The Golden Atlas: All the roads and streets in Israel: 104 cities and towns. Map - Mapping and publishing, Tel Aviv.
Road atlas 2009	Blinky, A. (2009). The Golden Atlas: All the roads and streets in Israel: 152 cities and towns. Map - Mapping and publishing, Tel Aviv.
Additional Orthophotos of several settlements	▪ Orthophoto 2002 of Bnei Shimon Regional Council- gis.bns.org.il/Gis/#/(main-side:layers). ▪ Orthophoto 2003 of Ness Ziona- mg2.gis-net.co.il/NessZionaGis/#/(main-side:layers). ▪ Orthophoto 1999 of Emek Yizra'el- mg2.gis-net.co.il/israelimGis ▪ Orthophoto 2002 of Rosh Ha'Ein- gisrh.taldor.co.il/Gis/#/(main-side:selection-results). ▪ Orthophoto 1965-2005 of Ramat Hasharon- gis.ramathasharon.muni.il. ▪ Orthophoto 2003 of Raanana- gis01.taldor.co.il/raananaNew/Default. aspx. ▪ Orthophoto 2001 of Pardes Hana- Karkur- mg1.gis-net.co.il/PardesHanaKarkurGis/#/main-side: layers.