Karadeniz Fen Bilimleri Dergisi, 11(2), 355-369, 2021. DOI: 10.31466/kfbd.835382

KFBD

Karadeniz Fen Bilimleri Dergisi
The Black Sea Journal of Sciences
ISSN (Online): 2564-7377

Araştırma Makalesi / Research Article

Detecting Barriers Between Protected Areas to Restore Ecological Connectivity†

Huriye Simten SÜTÜNÇ

Abstract

Protected areas have two tasks on a global scale: First, to protect biodiversity and second, to ensure the continuity of ecosystem services. Identifying potential links between protected areas in a region and barriers between these links or restoration points is very important for the effective development and implementation of conservation strategies within the scope of biodiversity. In this study firstly, potential connectivity corridors between 10 different protected areas were determined to support the biological diversity in the Rize landscape, then the barriers that could block the ecological flows in these corridors were determined by using 100 m, 500 m, 300 m radii. Least Cost Path and Cost Weighted Distance methods were used for both analyses. The most suitable corridors have been identified between Kaçkar Mountains National Park-1st Degree Natural Protected Areas-Wildlife Protection and Development Area and Firtina Creek. Improvement scores were calculated by considering the radii determined for the barriers. As a result, the highest improvement scores at 100 m, 500 m 300 m radii were calculated as 21.1, 4.49, and 7.0, respectively, and according to these scores, it showed that there were barriers between Karadere, Handüzü Nature Park, Uzungöl Special Environmental Protection Area and Kaçkar Mountains National Park. The method used in this study is important in terms of generating protection strategies for protected areas in the Rize landscape. The results of this study will guide not only protected areas in Rize landscape, but also conservation priority planning studies.

Keywords: Landscape connectivity, Protected areas, Barriers, Restoration opportunities, Improvement score, Biodiversity.

Ekolojik Bağlantılılığı İyileştirmek İçin Korunan Alanlar Arasındaki Bariyerlerin Belirlenmesi

Öz

Korunan alanların küresel ölçekte iki görevi vardır: Birincisi, biyolojik çeşitliliği korumak ve ikincisi, ekosistem servislerinin devamlılığını sağlamak. Bir bölgedeki korunan alanların birbirleri arasındaki potansiyel bağlantıların ve bu bağlantılar arasındaki engellerin ya da restorasyon noktalarının belirlenmesi, biyolojik çeşitlilik kapsamında koruma stratejilerinin etkin bir şekilde geliştirilmesi ve uygulanması açısından oldukça önemlidir. Bu çalışmada, Rize peyzajındaki biyolojik çeşitliliği desteklemek için önce, 10 farklı korunan alan arasındaki potansiyel bağlantı koridorları belirlenmiş, sonra bu koridorlardaki ekolojik akışları engelleyebilecek bariyerler 100 m, 500 m ve 300 m'lik tarama yarıçapları kullanılarak tespit edilmiştir. Her iki analiz için Least Cost Path ve Cost Weighted Distance yöntemleri kullanılmıştır. En uygun koridorlar, Kaçkar Dağları Milli Parkı-1. Derece Doğal Sit Alanları-Yaban Hayatı Koruma ve Geliştirme Sahası ile Fırtına Deresi arasında tespit edilmiştir. Bariyerler için belirlenen tarama yarıçapları dikkate alınarak iyileştirme puanları hesaplanmıştır. Sonuçta, 100 m, 500 m ve 300 m'lik yarıçaplarda en yüksek iyileştirme puanları sırasıyla 21.1, 4.49 ve 7.0 olarak hesaplanmış ve bu puanlara göre Karadere, Handüzü Tabiat Parkı, Uzungöl Özel Çevre Koruma Alanı ve Kaçkar Dağları Milli Parkı arasında bariyerlerin olduğunu göstermiştir. Bu çalışmada kullanılan yöntem, Rize peyzajındaki korunan alanlar için koruma stratejileri üretmek açısından önemlidir. Bu çalışmanın sonuçları sadece Rize peyzajındaki korunan alanlar için değil, öncelikli planlama çalışmalarında da yönlendirici olacaktır.

Anahtar Kelimeler: Peyzaj bağlantılılığı, Korunan alanlar, Bariyerler, Restorasyon fırsatları, İyileştirme puanı, Biyoçeşitlilik.

†This study was presented as abstract at 2nd International Symposium on Biodiversity Research, Rize, Turkey, 18-20 November 2020

Siirt University, Faculty of Agriculture Department of Landscape Architecture, Siirt, Turkey, simten.sutunc@siirt.edu.tr

https://orcid.org/0000-0002-0149-9953

Geliş/Received: 03.12.2020 **Kabul/Accepted:** 21.03.2021

1. Introduction

Protected areas play a critical role in protecting biodiversity. Well-planned, and managed protected areas help maintain ecosystem services by effectively protecting species and ecosystems. Connectivity of protected areas is a necessity for ecological and evolutionary processes (gene flow, migration, species movement, etc.) (Bingham et al., 2019; Castillo et al., 2020; Saura et al., 2018). All these processes are essential for all species facing climatic and environmental changes that increasingly transform and disintegrate landscapes. Therefore, ensuring the connectivity between protected areas is a fundamental problem for the effective protection and management of biological diversity (Corrigan et al., 2018; Jalkanen, Toivonen, & Moilanen, 2020; Santini, Saura, & Rondinini, 2016; Stewart, Darlington, Volpe, McAdie, & Fisher, 2019).

The term barrier is defined as a landscape feature that prevents movement between ecologically important areas and whose removal will increase the movement potential between these areas (Carroll, McRae, & Brookes, 2012; Panzacchi et al., 2016). Barriers can be man-made (roads, etc.) or natural (rivers, streams, canyons, etc.) and, unlike corridors, it has the feature of blocking movement and ecological flow. As it is the case in other ecological situations, what constitutes a barrier to species and habitats may differ (Taylor, Fahrig, Henein, & Merriam, 1993; Tischendorf & Fahrig, 2000). Identifying barriers that exist along corridors that enable the movement of species is an integral part of corridor/linkage analysis. Knowing where barriers have the greatest impact will help practitioners how to invest in what protection resources to maintain and improve connections. For example, it may be more appropriate to restore a barrier that blocks the movement corridor across public land than to permanently maintain a functioning corridor that runs through private land (Baldwin, Perkl, Trombulak, & Burwell, 2010). Analysing such risks and gains will be necessary to integrate 1st, link restoration into systematic conservation-planning analysis aimed at improving conservation investments (Margules & Pressey, 2000; Wilson et al., 2007). 2nd, barrier analysis can reveal risk-acquisition situations, allowing practitioners to distinguish a land according to its characteristics, directing the work to be done to more appropriate action points.

In this study, potential corridors between 10 different protected areas in the Rize landscape and barriers that could prevent the movement of species along these corridors were analysed. Linkage Mapper programme (McRae & Kavanagh, 2011) was used to identify links/corridors between protected areas. The programme integrates Least-Cost-Path (LCP) and Cost-Weighted-Distance (CWD) methods with core area data and resistance maps, calculates the least costly distances between existing core areas and determines connectivity corridors. Barriers between corridors connecting protected areas are identified with the Barrier Mapper programme (McRae, Hall, Beier, & Theobald, 2012). The programme obtains barrier effect or restoration improvement scores for a link by estimating reductions in the least-cost-distance with the lowest cumulative cost of movement between the respective core pair. It uses different scan radii to calculate these scores. Where the improvement score is maximum, removing the barrier will re-route the best course of action, for example by building a wildlife crossing structure. In the study in question, 100 m, 500 m, and 300 m radius values were used to determine the barriers between protected areas. As a result, the highest improvement scores at 100 m, 500 m, and 300 m radii were calculated as 21.1, 4.49, and 7.0, respectively. It has been determined that there are barriers between Kaçkar Mountains National Park, Uzungöl Special Environmental Protection Area (SEPA) in the southwest, Karadere and Handüzü Nature Park. At the same time, the LCP values of the links between these areas are also very high. High LCP means low connectivity. The method used in this study is important for generating conservation strategies for protected areas in the Rize landscape. The results of this study will guide not only protected areas in the Rize landscape but also conservation priority planning studies.

2. Materials and Methods

2.1. Material

Rize is located in the Eastern Black Sea Region of Turkey, at 41.0255 north, and 40.5177 south latitudes (Figure 1). In this study, honey production forest, gene protection areas, seed stands, natural protected areas, nature parks, natural areas, national park, wildlife protection and development areas, and SEPA within the provincial borders are evaluated within the scope of the protected areas. The protected areas selected for barrier analysis are shown in Figure 2.

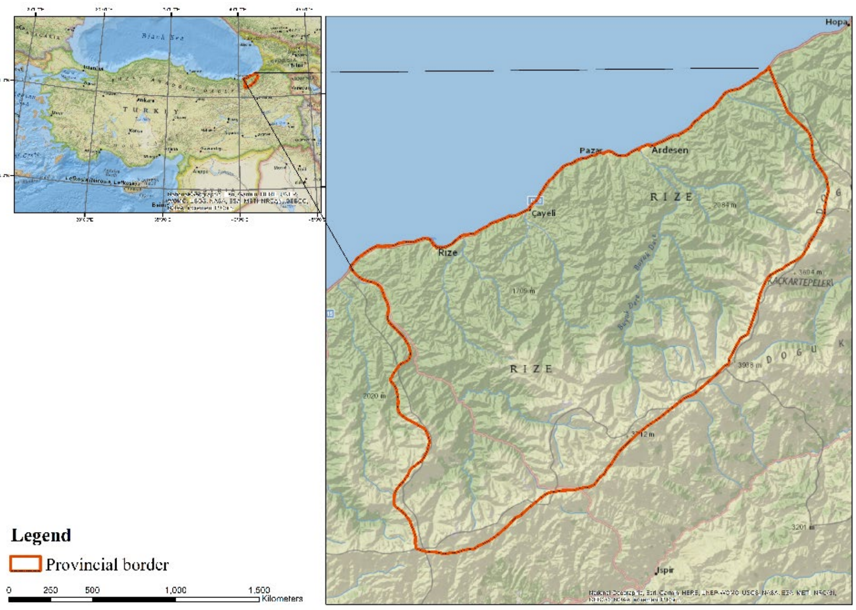


Figure 1. Geo-location of Rize.

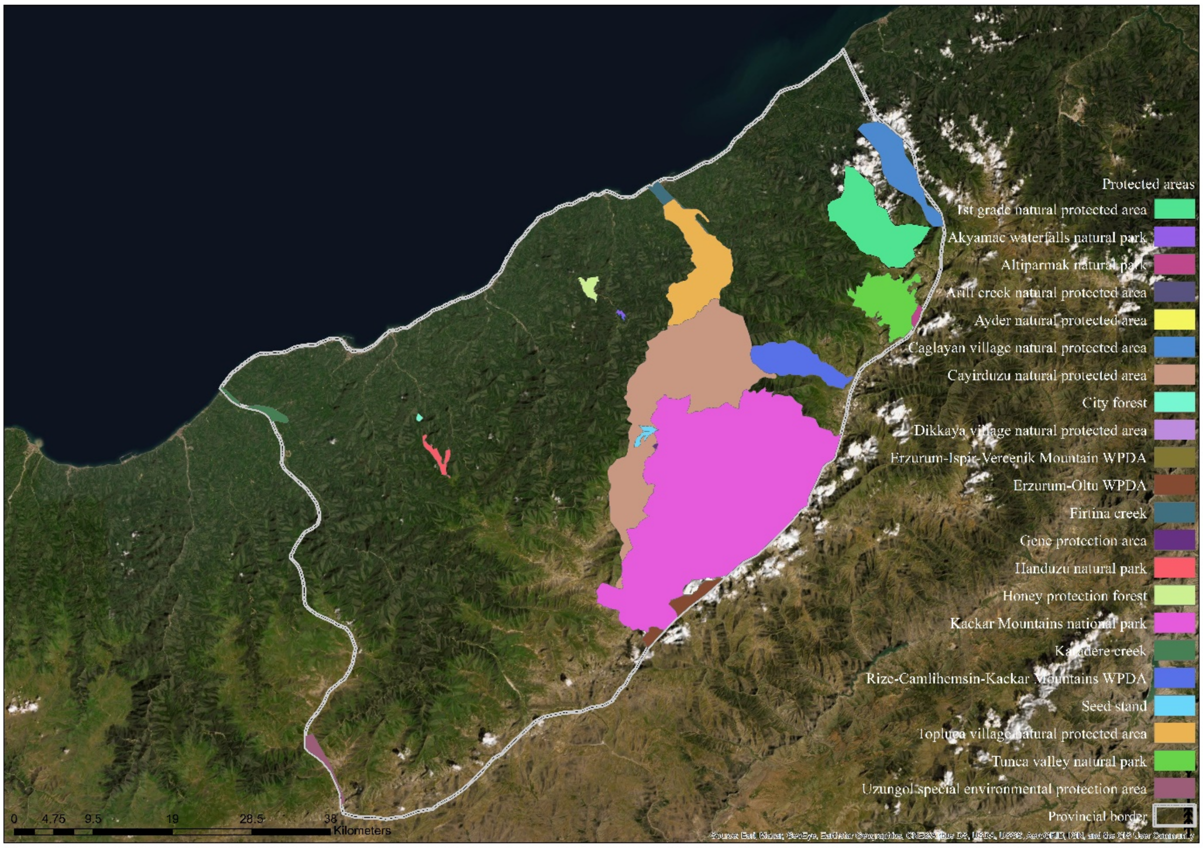


Figure 2. Protected areas of Rize.

2.2. Methods

Barriers are areas where landscape features inhibit wildlife movement between core areas and habitats. For barrier analysis, it is essential to determine the corridors first. The LCP analysis has been performed in order to maintain connectivity and prioritise important areas in this regard (Adriaensen et al., 2003; Carroll et al., 2012; Knaapen, Scheffer, & Harms, 1992; Singleton, Gaines, & Lehmkuhl, 2002). Linkage Mapper programme developed by McRae and Kavanagh (2011) was used for the corridor analysis. In the first step of the method, core area data -protected areas are defined as core areas in this study- and resistance map is used as input. Resistance surfaces in the resistance map represent the difficulty for wildlife movement. Energy cost or risk of death associated with movement along each pixel (Zeller, McGarigal, & Whiteley, 2012). The LCP methods used to create corridors create a raster of CWD values by calculating the CWD of all pixels to the source area. Combining CWD raster obtained from the distance between the two areas, a corridor is created that shows the paths with the lowest cumulative movement cost (Adriaensen et al., 2003). The lowest value of the corridor raster is the LCP, this represents the cumulative resistance encountered when moving along the path best suited from one location to another and is considered a common insulation measure for the areas concerned (Chardon, Adriaensen, & Matthysen, 2003; Cushman, McKelvey, Hayden, &

Schwartz, 2006; Graham, 2001; Schwartz et al., 2009). Barrier analysis was carried out in conjunction with the method used for corridor analysis. For this, the Barrier Mapper programme developed by (McRae et al., 2012) was used. In addition to the inputs used for corridor analysis, the programme asks the user to specify a scan radius. The lower the LCP values at the nodes where the most suitable corridor between the patches/core areas is connected in the previous stage, the lower resistance values will be. In a landscape, systematically low measurement of LCP values within the specified scanning radii will ensure the determination of the areas that will provide the most gain at the lowest cost of the restoration. The lowest CWD between each protected area, which is the subject of this study, were calculated by determining the scanning radii of 100 m, 500 m, and 300 m. Then, the cumulative resistance between the areas within the scanning radius was calculated and the lowest CWD values were added to this cumulative resistance (McRae et al., 2012). As a result of this calculation, improvement scores were calculated. Removing the barriers in the places where the improvement score is the highest provides the re-orientation of the connectivity between the two areas.

3. Findings and Discussion

3.1. Landscape Connectivity Analysis

LCP and CWD values measured across protected areas determine the basis of the corridor connections. Low LCP (path where least resistance accumulates) value means easier movement and ecological flow for the species. Connections and corridors created by calculating CWD and LCP values using the Linkage Mapper programme (McRae & Kavanagh, 2011) are shown in Figure 3. The CWD value between Kaçkar Mountains National Park – Çayırdüzü 1st Degree Natural Protected Area and Arılı Stream 1st Degree Natural Protected Area and Erzurum-Oltu Wildlife Development Area – Arılı Stream 1st Degree Natural Protected Area (10 m). The cumulative resistance in these areas is very low and seems quite suitable for the wildlife corridor. Cumulative resistance has been calculated the most among Karadere – Uzungöl SEPA – Çayırdüzü 1st Degree Natural Protected Area. The links between these areas pose a risk for the movement of the species. The areas seen in pink (108.684 m), in the raster CWD map created with the calculations are areas that are impossible in terms of connectivity and are at risk of death for the movement of the species. The same result can be seen in the LCP map. The red coloured areas (186.819 m) on the relevant map indicate the risky areas for corridor formation. Areas with a value of 0 (zero) in both maps are potential corridors where links can be created. LCP values also support CWD values. LCP values between Karadere – Uzungöl SEPA – Kaçkar Mountains National Park were calculated as 48.250 m and 41.344 m, respectively. The links between these areas cover the riskiest paths for species movement. The links where the movement will be the easiest and the most risk-free are calculated between the National Park – Natural Protected Areas – Wetlands – Wildlife Development Areas. LCP values between these areas are 10 m.

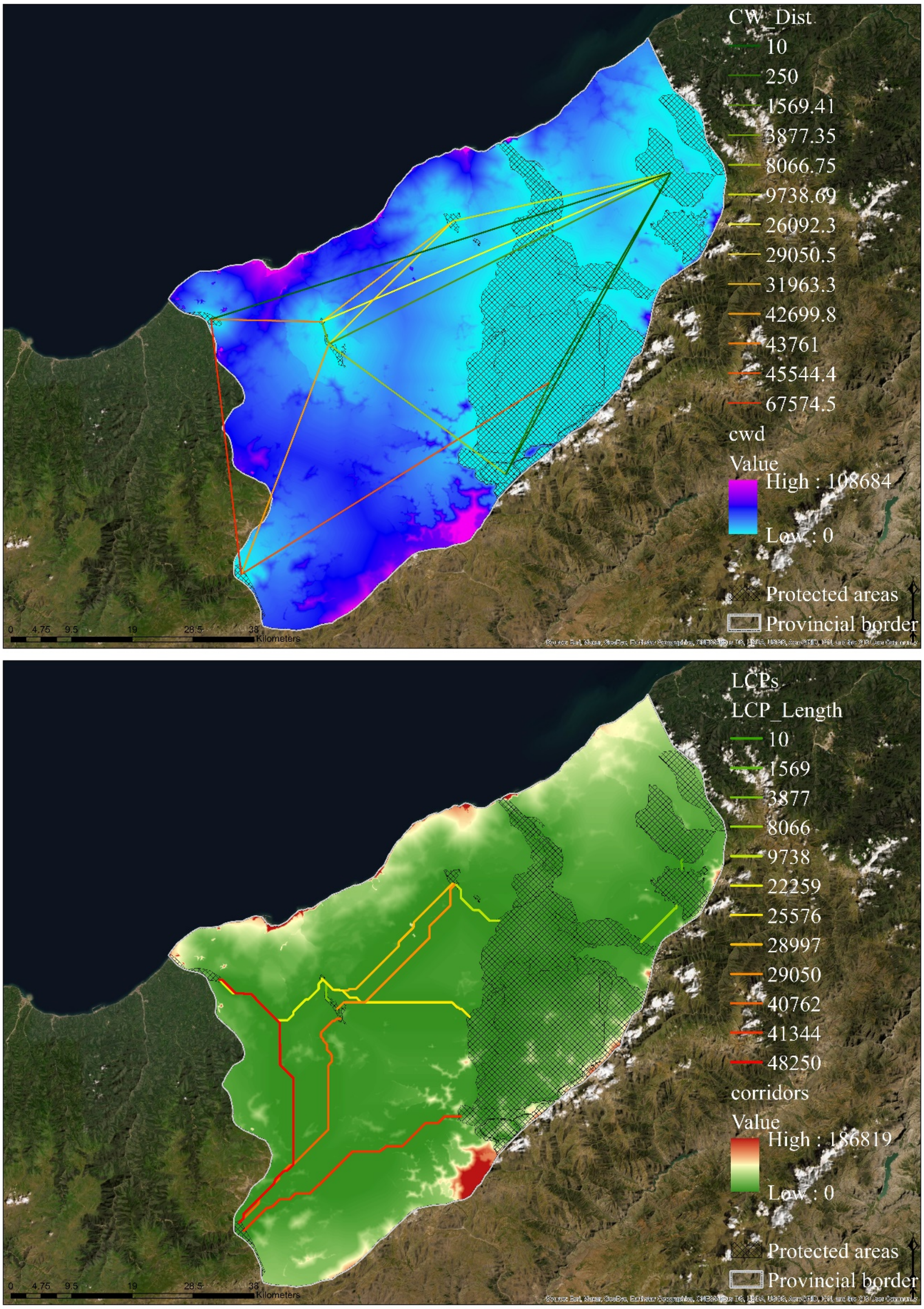


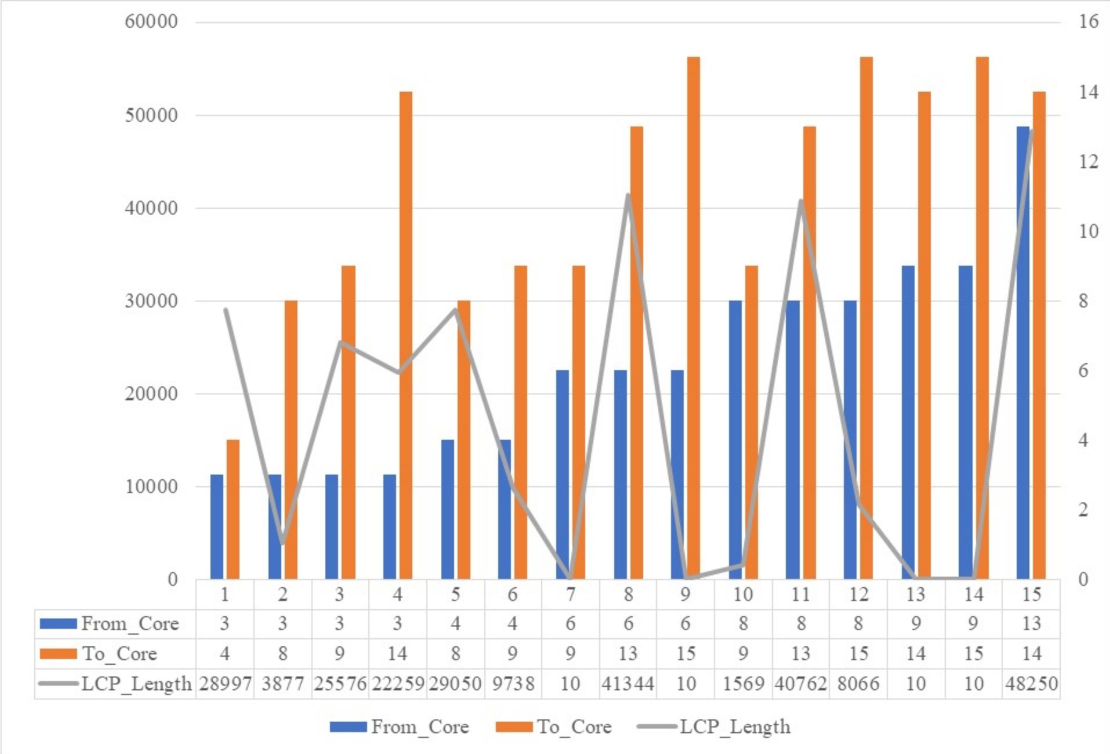
Figure 3. CWD and LCP values of protected areas, respectively.

The results of this study regarding the connectivity of the landscape reveal that the cumulative resistance of the corridors between the interlocking protected areas is less and the connectivity value is higher. In the concept of connectivity, the functional link between populations is facilitated while structurally similar patches and habitats are connected to each other (Stewart et al., 2019). Calculation of LCP and CWD values shows to what extent the resistances along the corridor can affect the ecological flow (McRae & Kavanagh, 2011). LCP and CWD values calculated for National Park, 1st Degree Natural Protected Areas, Wetland, and Wildlife Development Area show the shortest corridor that can be created between the areas, the smoothest ecological flow and therefore the easiest connection. The further the fields are from each other and the more structures that serve as stepping stones are missing, the more difficult the movement and flow of species will be (Figure 4).

The distance and cumulative resistance between the Wetland, SEPA, and 1st Degree Natural Protected Area is the highest. Stepping stones are structures by which species can move short distances between patches found in the landscape matrix. Species moving in a matrix without a stepping stone will travel longer along the matrix and face greater risk (Forman, 1995; Stewart et al., 2019). When the connectivity between protected areas in the study area is examined, it has been revealed that the connection between the protected areas is more easily established due to the existence of structures whose boundaries are within each other and serve as stepping stones.

On the other hand, the connection between the protected areas, where the distance between them and therefore the cumulative resistance is high, was weak. It can be counted among the results that a single protected area in a matrix has little effect on landscape connectivity. Ensuring the continuity and therefore the ecological integrity of protected areas is critical for species to establish connections in the landscape to support biological diversity (Castillo et al., 2020; Jalkanen et al., 2020; Santini et al., 2016; Saura et al., 2018).

Another factor affecting the connectivity between protected areas is land cover/land use (Tesfaw et al., 2018). When the map in Figure 5 is examined, it is seen that the land cover/land use type with the best connecting protected areas is forest matrix (coniferous, broad-leaved and mixed). Transitional woodland-shrub, pastures, fruit trees and berry plantations, and agricultural areas have negatively affected the potential corridor to be created between the fields in areas of distance.



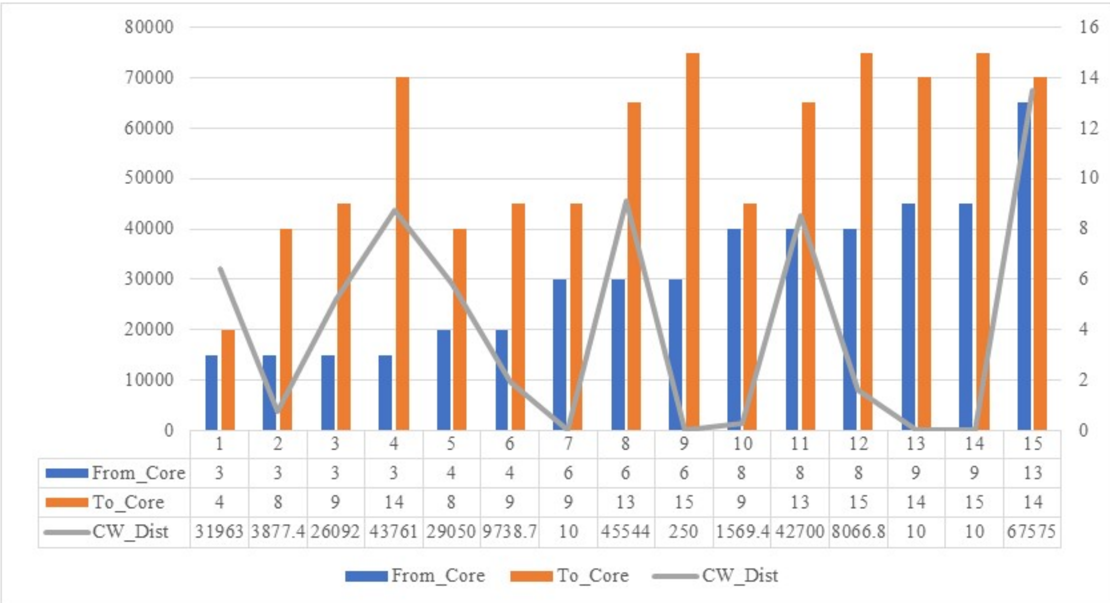


Figure 4. LCP and CWD values for protected areas, respectively.

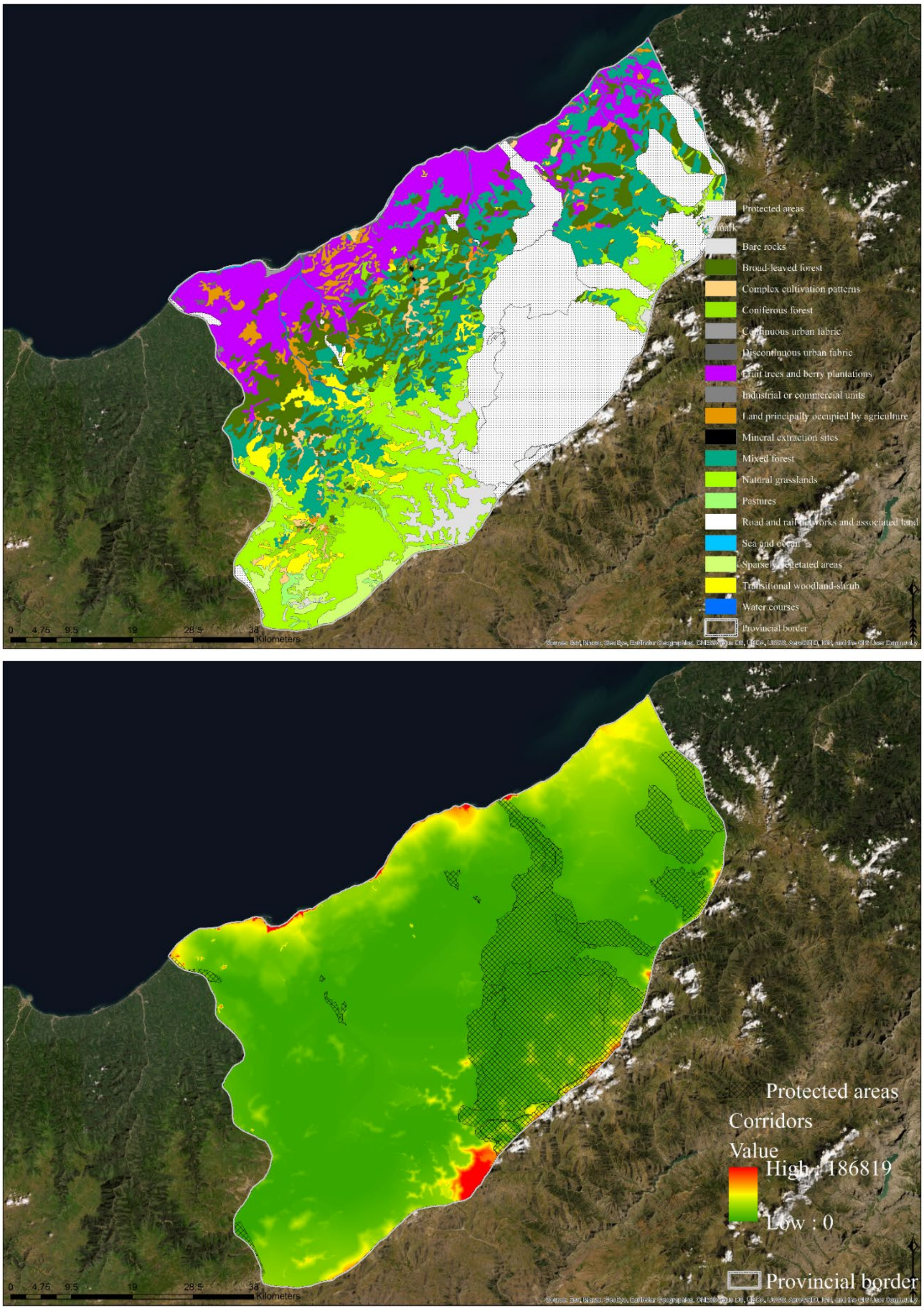


Figure 5. Land use/land cover and connectivity corridors between protected areas.

3.2. Barrier Analysis

Barrier is a landscape feature that prevents movement between ecologically important areas and its removal will increase the movement potential between these areas. Barrier means the opposite of corridors. Scanning radii of 100 m, 500 m, and 300 m were created in order to determine the barriers between the protected areas selected for analysis. The improvement scores were calculated to include both the centre of the resistive pixel and the scan radius according to the LCP values at each radius. It was observed that barriers were formed in the southwest of Kaçkar Mountains National Park, in the northeast and west of Handüzü Nature Park in a scanning radius of 100 m. The highest improvement score for this scan radius is calculated as 21. Improvement score in the same scanning radius compared to the LCP value is 0.1% as a percentage.

In the calculation in which the scanning radius was selected as 300 m, barriers were found in the southeast of Karadere, southeast of Kaçkar Mountains National Park, and east and west of Handüzü Nature Park. In this scanning radius, the improvement score is 7.0 and as a percentage, it is 0.02%.

In the case the radius is 500 m, it is seen that the barrier calculations made with a radius of 300 m gain precision. The barriers between Karadere, Handüzü Nature Park, and Kaçkar Mountains National Park have become quite effective. In addition to these, it was revealed that barriers were formed between Akyamaç Waterfall Nature Park and Honey Production Forest. The highest improvement score in this radius was 4.49, the percentage reflection of this score on the LCP value was 0.01%. The status of the barriers between the protected areas in the scanning LCP value was 0.01%. The status of the barriers between the protected areas in the scanning radii of 100 m, 300 m, and 500 m and the LCP values between the protected areas are shown in Figure 6.

The results of the barrier analysis of this study showed that there are barriers and new barriers between Kaçkar Mountains National Park, Handüzü Nature Park, Karadere and Uzungöl SEPA. It is noteworthy that the barriers especially follow the streams and river lines. It can be concluded that the negative effects caused by the Hydroelectric Power Plant (HEPP) projects, especially in the Black Sea Region, show itself as a barrier between the protected areas in Rize (Figure 7).

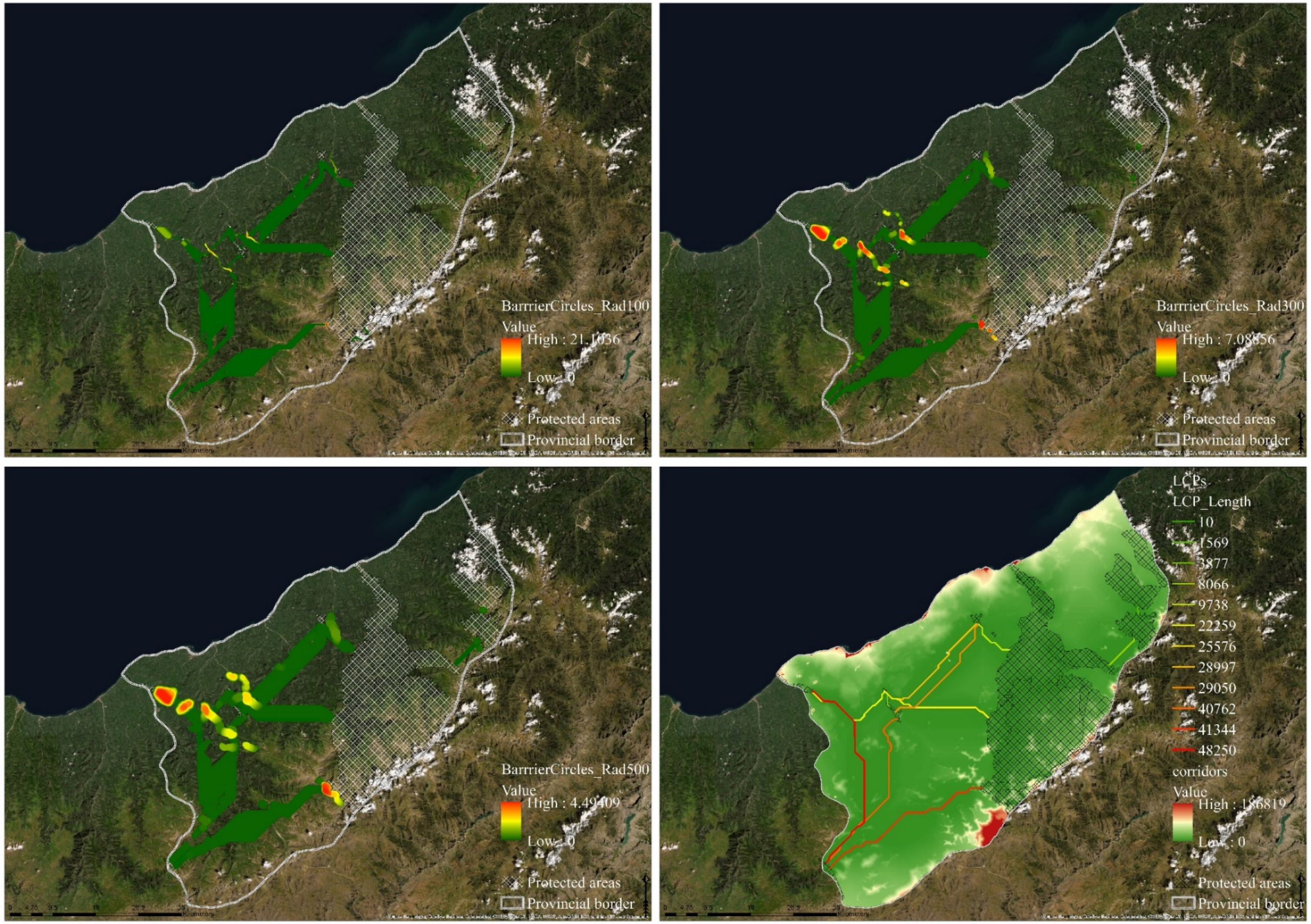
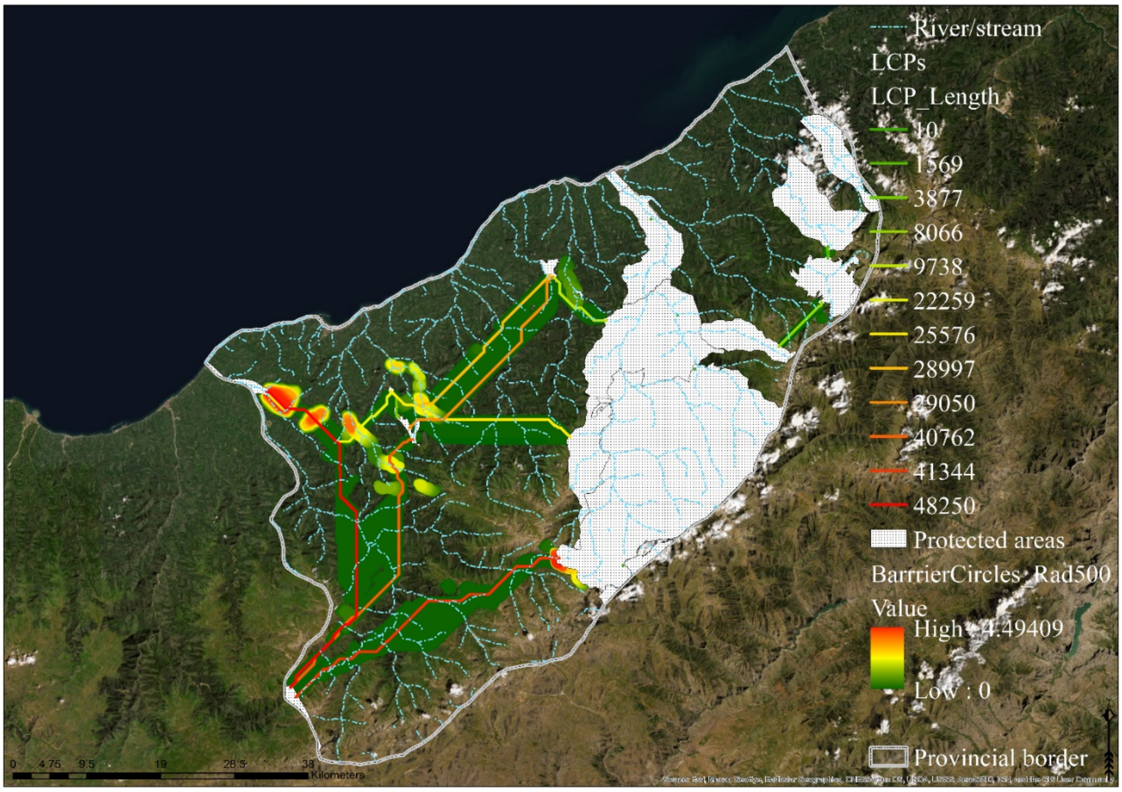
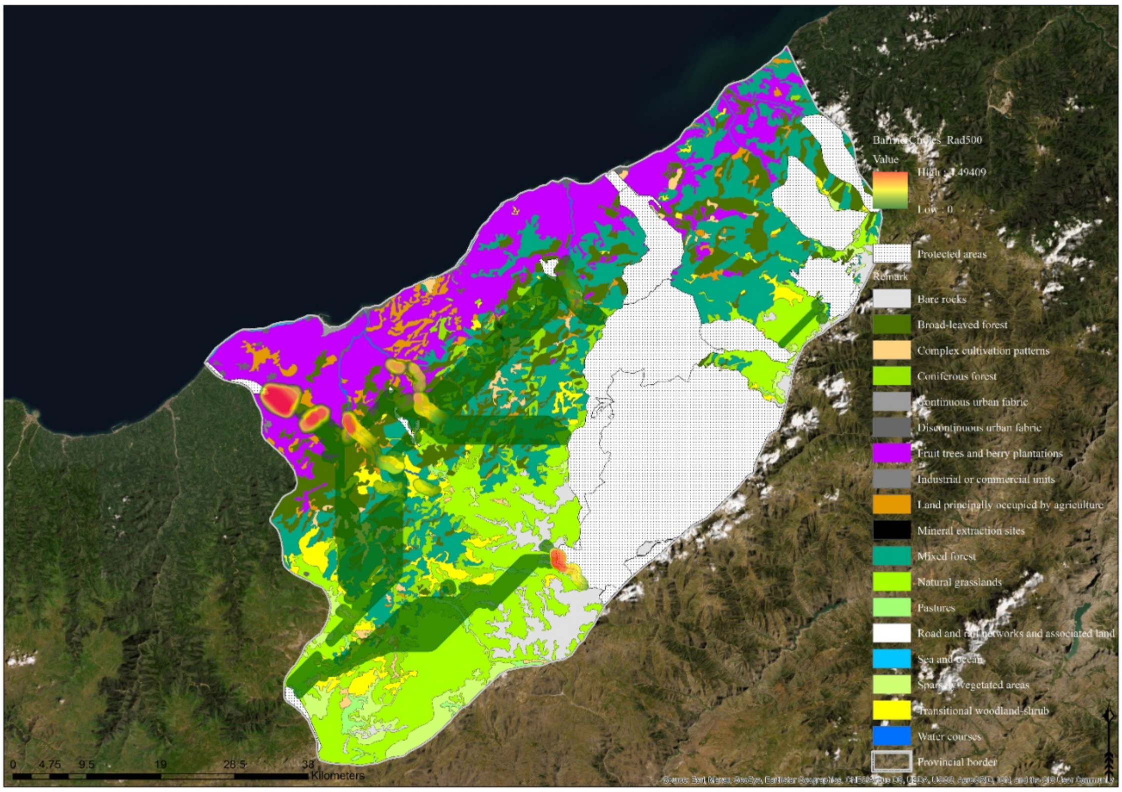


Figure 6. Land use/land cover and connectivity corridors between protected areas.





As long as the natural system interacts with each other, it is in balance. One or more barrier effects can be mentioned at the points where the interaction is interrupted. In addition, these barriers can be either natural or man-made (McRae et al., 2012). On the other hand, there was no restrictive effect among the natural sites in the east of Rize. Although barrier literally refers to a barrier, its use for landscape refers to areas that make the passage of wildlife difficult, but where the ecological flow will be the best when restored. Therefore, the barrier areas analysed in the Rize landscape are areas where energy, material, etc. flows between species will be best when an ecological restoration applications are made. Identifying these areas shows how to increase the protection options available to practitioners, provide a better understanding of analysis products and result in more robust conservation plans. The most important result of the analysis is that a new corridor has been formed between Akyamaç Waterfall Nature Park, Honey Production Forest, and Çayırdüzü 1st Degree Natural Site. This is an important consequence because organisms/species rarely achieve movement using a single link, and the extra linkages help ensure sustained connectivity in the face of unpredictable environmental changes (McRae, Dickson, Keitt, & Shah, 2008; Pinto & Keitt, 2009). The analysis also, showed that maintaining the link between protected areas and conservation strategies need not be limited to a small part of the landscape, opens much more space for actions that can preserve or improve links, and that a balance between different conservation strategies and objective can be achieved.

4. Conclusions and Recommendations

From the moment it started to exist until today and in the future, the human has prioritised and will keep its own needs in order to survive. The depletion of natural resources on a global scale and the decrease in biological diversity also support this idea. The rapidly decreasing natural vegetation, increasing intensive land uses cause the loss of landscape connectivity necessary for the continuation of wildlife and biodiversity and manifests itself as an element of pressure in landscape. Hence, restoring connectivity is important to maintain the system and to support biodiversity. Protected areas are areas where biological diversity is found in the widest sense. On the other hand, just conducting connectivity analysis is not enough to rebuild ecosystem functioning. An existing barrier (man-made or natural) between corridors will also disrupt the continuity of the system.

In this study, potential landscape connectivity corridors between protected areas in the Rize landscape and possible barriers in these corridors were determined. In addition to its negative meaning as “obstacle”, the term barrier has taken its place in this analysis as the structure that increases the restoration opportunities at the point where it is removed and the ecological flow in the corridor connectivity will be optimised. In the landscape of Rize, it is noteworthy that there are barriers along the stream/river structures that connect the protected areas and functions as natural corridors. This is thought to be due to the increasing construction of HEPP structures in recent years and the changing land cover/land uses. Making the blockages at the barrier points re-permeable by taking effective measures such as ecological restoration will mean that the whole system working together will regain its functionality. On the other hand, the system also tended to create different connections in order to keep itself in balance. The formation of a new corridor between Akyamaç Waterfall Nature Park, Honey Production Forest and Çayırdüzü 1st Degree Natural Site is an example. It is a fact that the strategies implemented regarding protected areas, whose protection is guaranteed by agreements made at both national and international levels, are not sufficient on a global scale. Actively, including the decisions with protection priority in the legal and administrative processes of the countries and measuring the success of the implementations with an effective control mechanism will bring positive results in terms of protected areas and biodiversity.

Authors' Contributions

All authors contributed equally to the study.

Statement of Conflicts of Interest

There is no conflict of interest between the authors.

Statement of Research and Publication Ethics

The author declares that this study complies with Research and Publication Ethics.

References

Adriaensen, F., Chardon, J. P., De Blust, G., Swinnen, E., Villalba, S., Gulinck, H., & Matthysen, E. (2003). The application of 'least-cost' modelling as a functional landscape model. *Landscape and Urban Planning, 64*(4), 233-247. doi:https://doi.org/10.1016/S0169-2046(02)00242-6

Baldwin, R. F., Perkl, R. M., Trombulak, S. C., & Burwell, W. B. (2010). Modeling Ecoregional Connectivity. In S. C. Trombulak & R. F. Baldwin (Eds.), *Landscape-scale Conservation Planning* (pp. 349-367). Dordrecht: Springer Netherlands.

Bingham, H. C., Juffe Bignoli, D., Lewis, E., MacSharry, B., Burgess, N. D., Visconti, P., . . . Kingston, N. (2019). Sixty years of tracking conservation progress using the World Database on Protected Areas. *Nature Ecology & Evolution, 3*(5), 737-743. doi:10.1038/s41559-019-0869-3

Carroll, C., McRae, B. H., & Brookes, A. (2012). Use of linkage mapping and centrality analysis across habitat gradients to conserve connectivity of Gray wolf populations in Western North America. *Conservation Biology, 26*(1), 78-87.

Castillo, L. S., Correa Ayram, C. A., Matallana Tobón, C. L., Corzo, G., Areiza, A., González-M..R., . . . Godínez-Gómez, O. (2020). Connectivity of protected areas: Effect of human pressure and subnational contributions in the ecoregions of tropical Andean Countries. *Land, 9*(8), 239. Retrieved from https://www.mdpi.com/2073-445X/9/8/239

Chardon, J. P., Adriaensen, F., & Matthysen, E. (2003). Incorporating landscape elements into a connectivity measure: a case study for the Speckled wood butterfly (Pararge aegeria L.). *Landscape Ecology, 18*(6), 561-573. doi:10.1023/A:1026062530600

Corrigan, C., Bingham, H., Shi, Y., Lewis, E., Chauvenet, A., & Kingston, N. (2018). Quantifying the contribution to biodiversity conservation of protected areas governed by indigenous peoples and local communities. *Biological Conservation, 227*, 403-412. doi:https://doi.org/10.1016/j.biocon.2018.09.007

Cushman, S. A., McKelvey, K. S., Hayden, J., & Schwartz, M. K. (2006). Gene flow in complex landscapes: testing multiple hypotheses with causal modeling. *The American Naturalist, 168*(4), 486-499. doi:10.1086/506976

Forman, R. T. T. (1995). *Land mosaics : The Ecology of Landscapes and Regions* Cambridge ; New York: Cambridge University Press.

Graham, C. H. (2001). Factors influencing movement patterns of Keel-Billed Toucans in a fragmented tropical landscape in Southern Mexico. *Conservation Biology, 15*(6), 1789-1798. Retrieved from http://www.jstor.org/stable/3061279

Jalkanen, J., Toivonen, T., & Moilanen, A. (2020). Identification of ecological networks for land-use planning with spatial conservation prioritization. *Landscape Ecology, 35*(2), 353-371. doi:10.1007/s10980-019-00950-4

Knaapen, J. P., Scheffer, M., & Harms, B. (1992). Estimating habitat isolation in landscape planning. *Landscape and Urban Planning, 23*(1), 1-16. doi:https://doi.org/10.1016/0169-2046(92)90060-D

Margules, C. R., & Pressey, R. L. (2000). Systematic conservation planning. *Nature, 405*(6783), 243-253. doi:10.1038/35012251

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. doi:10.1890/07-1861.1

McRae, B. H., Hall, S. A., Beier, P., & Theobald, D. M. (2012). Where to restore ecological connectivity? Detecting barriers and quantifying restoration benefits. *PLOS ONE, 7*(12), e52604. doi:10.1371/journal.pone.0052604

McRae, B. H., & Kavanagh, D. M. (2011). Linkage Mapper Connectivity Analysis Software. Retrieved from http://www.circuitscape.org/linkagemapper.

Panzacchi, M., Van Moorter, B., Strand, O., Saerens, M., Kivimäki, I., St. Clair, C. C., . . . Boitani, L. (2016). Predicting the continuum between corridors and barriers to animal movements using Step Selection Functions and Randomized Shortest Paths. *Journal of Animal Ecology, 85*(1), 32-42. doi:10.1111/1365-2656.12386

Pinto, N., & Keitt, T. H. (2009). Beyond the least-cost path: evaluating corridor redundancy using a graph-theoretic approach. *Landscape Ecology, 24*(2), 253-266. doi:10.1007/s10980-008-9303-y

Santini, L., Saura, S., & Rondinini, C. (2016). Connectivity of the global network of protected areas. *Diversity and Distributions, 22*(2), 199-211. doi:10.1111/ddi.12390

Saura, S., Bertzky, B., Bastin, L., Battistella, L., Mandrici, A., & Dubois, G. (2018). Protected area connectivity: Shortfalls in global targets and country-level priorities. *Biological Conservation, 219*, 53-67. doi:https://doi.org/10.1016/j.biocon.2017.12.020

Schwartz, M. K., Copeland, J. P., Anderson, N. J., Squires, J. R., Inman, R. M., McKelvey, K. S., . . . Cushman, S. A. (2009). Wolverine gene flow across a narrow climatic niche. *Ecology, 90*(11), 3222-3232. doi:10.1890/08-1287.1

Singleton, P. H., Gaines, W., & Lehmkuhl, J. (2002). *Landscape permeability for large carnivores in Washington: a geographic information system weighted-distance and least-cost corridor assessment*.

Stewart, F. E. C., Darlington, S., Volpe, J. P., McAdie, M., & Fisher, J. T. (2019). Corridors best facilitate functional connectivity across a protected area network. *Scientific Reports, 9*(1), 10852. doi:10.1038/s41598-019-47067-x

Taylor, P. D., Fahrig, L., Henein, K., & Merriam, G. (1993). Connectivity is a vital element of landscape structure. *Oikos, 68*, 571-573.

Tesfaw, A. T., Pfaff, A., Golden Kroner, R. E., Qin, S., Medeiros, R., & Mascia, M. B. (2018). Land-use and land-cover change shape the sustainability and impacts of protected areas. *Proceedings of the National Academy of Sciences, 115*(9), 2084-2089. doi:10.1073/pnas.1716462115

Tischendorf, L., & Fahrig, L. (2000). On the usage and measurement of landscape connectivity. *Oikos, 90*(1), 7-19. doi:10.1034/j.1600-0706.2000.900102.x

Wilson, K. A., Underwood, E. C., Morrison, S. A., Klausmeyer, K. R., Murdoch, W. W., Reyers, B., . . . Possingham, H. P. (2007). Conserving biodiversity efficiently: What to do, where, and when. *PLOS Biology, 5*(9), e223. doi:10.1371/journal.pbio.0050223

Zeller, K. A., McGarigal, K., & Whiteley, A. R. (2012). Estimating landscape resistance to movement: a review. *Landscape Ecology, 27*(6), 777-797. doi:10.1007/s10980-012-9737-0