Web Ecol., 13, 91–93, 2013
www.web-ecol.net/13/91/2013/
doi:10.5194/we-13-91-2013

Open Access
Web Ecology

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The "four-color issue" in ecology for considering ecosystem boundaries

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Received: 1 July 2013 – Revised: 2 October 2013 – Accepted: 23 October 2013 – Published: 28 October 2013

Abstract. Ecosystem boundaries are important structures in defining ecosystems. To date, ecologists have not extensively considered which boundaries are important in explaining ecological phenomena in order to simplify ecological theories. The four-color theorem in mathematics maintains that only four colors are required to color a set of regions so that no two adjacent regions have the same color. Before being proven in 1976, the theorem was considered the "four-color issue", which proposed that a small number of colors were required to separate regional boundaries. Applying the principle of "four-color issue" to the ecological field, we can also examine reducing the number of ecosystem boundaries considered. That is, we can ask ourselves the following question: "how many boundaries of an ecosystem should be considered for ecology"? Here, I suggest a principle of ecosystem boundaries as the "four-color issue of ecology", and propose that this will be an important step toward advancing knowledge in ecology and conservation biology. In addition, I introduce graph theory, developed from the four-color theorem, which can be useful for estimating ecosystem boundaries.

1 Introduction

The ecosystem, defined by Tansley (1934), is an important framework describing the spatial structure of habitats in ecology. Tansley introduced the concept of the ecosystem as a system including inhabiting organisms and the entire complex of environmental factors characterizing the system (i.e., organisms and environmental factors interact within ecosystems). Ecosystem boundaries arise in various ways and are generally defined based on either physical or functional criteria (Puth and Wilson, 2001; Wiens, 2002; Strayer et al., 2003; Schultz et al., 2011). The ecosystem concept and ideas about ecosystem boundaries are widely disseminated in textbooks and ecological papers. However, unresolved issues regarding ecosystem boundaries (i.e., methods for defining these boundaries) have been noted (Post et al., 2007).

Numerous ecological studies have emphasized the importance of multiple ecosystem boundaries for community, food web, and ecosystem functions. For example, stream food webs are reciprocally connected to those of riparian forests across ecosystem boundaries through the movement of organisms (Nakano and Mukarami, 2001), and the ecosystem functions of agriculture fields are maintained by nearby natural habitats, such as forests and grasslands, and by water and pollinator resources beyond the ecosystem boundaries (Brosi et al., 2008). However, the issues regarding which boundaries are important or which boundaries should be taken into consideration when examining ecological phenomena have not been adequately addressed. Here, I pose a new question for the discussion on ecosystem boundaries: how many boundaries of an ecosystem should be considered for ecology? I examine this question with reference to the "four-color theorem (issue)" principle in mathematics.

2 The four-color theorem (issue) in mathematics

The "four-color theorem" is a well-known theorem in mathematics (Wilson, 2004). This theorem maintains that, given any separation of a plane into contiguous regions on a map, no more than four colors are required to color the regions such that no two adjacent regions have the same color. In 1852, Francis Guthrie suggested the four-color issue. Appel and Haken (1977a, b) proved this issue using computer simulation. This mathematical concept was historically called the "four-color issue", and many mathematicians have attempted to prove the theorem, which remains unresolved (Wilson, 2004).

Although the "five-color theorem", in which a map is painted by five colors, can be proved relatively easily, mathematicians have spent 12 decades attempting to prove the four-color theorem. In some scientific disciplines, including biology, the four-color theorem is utilized effectively, as in the analysis of graphical patterns of self-organization and cell topology (Chae et al., 2010). Chae et al. (2010) applied the four-color theorem to determine organization patterns of cells using two-dimensional maps.

After resolving the four-color theorem, graph theory in the three-dimensional world has been developed and begun to be applied in ecology. Graph theory is a mathematical concept concerned explicitly with connectivity in the 2- and 3-dimensional world. Graph theory has recently been undergoing explosive growth in many disciplines, including landscape ecology and conservation biology (Urban et al., 2009).

3 The four-color issue in ecology for reconsidering ecosystem boundaries

From the story of proving the "four-color issue" in mathematics, ecologists can recognize the importance of simplifying the way in which ecosystem boundaries are considered in the context of ecological theory. For the simplification of theories and modeling in ecology, we can use the scientific principle of "Occam's razor" (Ariew, 1976), which reduces the number of factors (boundaries here) to explain a scientific pattern. In the case of ecosystem boundaries, however, we should consider the spatial structure of ecosystem boundaries, such as stream–forest, stream–groundwater, and upstream–downstream boundaries. Thus, it is not simply a case of reducing a large number of ecosystem boundaries according to "Occam's razor", which reduces the unimportant factors to explain a pattern. We should also take into account the spatial structure of ecosystem boundaries, for example, by using the graph theory, which considers the spatial structure and connection of a map. According to graph theory, ecosystem boundaries should have numerous types of connections in three dimensions of connectivity (e.g., connections of canopy forest–stream, stream–groundwater, and upstream–downstream). Urban et al. (2009) suggested using structural connectivity of ecosystem boundaries to describe physical features of landscapes such as forest patches, hedgerows, and other elements obvious to the human eye. Graph theory is implemented to estimate ecosystem boundaries and connectivity using a modeling approach. Graphical models can provide a versatile representation of ecosystem mosaics and can provide insight into a variety of ecological questions at both the patch and landscape level (Urban et al., 2009).

To date, ecologists have mainly focused on multiple boundaries of ecosystems. Lamberti et al. (2010) pointed out that the number of boundaries recognized in aquatic ecosystems has increased in recent decades, indicating increasing ecological knowledge and understanding. It is important to continue to extend our knowledge; at the same time, we should move toward reducing the number of ecosystem boundaries considered in describing ecological phenomena, and toward a simplification of ecological theories. Therefore, we should consider the number of boundaries with reference to their importance. Here, I call the concept of reducing the large number of ecosystem boundaries the "four-color issue in ecology", with reference to the mathematical concept for coloring of maps.

To reduce the number of ecosystem boundaries considered, we need to know the relative importance of each boundary in an ecosystem. If the importance of a boundary is limited to a particular ecological phenomenon, the model to predict boundary transfer can exclude the less important boundary when considering that particular phenomenon. I suggest three potential means of determining the importance of ecosystem boundaries. Firstly, we need to track the flow of resources, energy, and organisms across ecosystem boundaries to define the importance of the boundaries to ecosystem and community/population dynamics. Examples include resource subsidies between forest and stream ecosystems (Nakano et al., 1999; Sato et al., 2012), and between terrestrial and lake ecosystems (Cole et al., 2006). Secondly, there is a need to compare internal and external ecosystem processes and the ratio of these processes for ecological functins (Post et al., 2007). If a boundary has a higher contribution of external processes, then that boundary should be considered important. Thirdly the importance of ecosystem boundaries should also be evaluated economically (i.e., the contributions to ecosystem services and functions). The use of simulation and field experiments that control the connections between ecosystem boundaries can facilitate evaluation of the economic values of the connections of a particular ecosystem boundary (e.g., Kozak et al., 2011).

As an example of considering the reduction of ecosystem boundaries, Muehlbauere et al. (2013) suggested using the spatial extent of the potential "stream signature" in terrestrial food webs. They found stream–terrestrial boundaries with various stream contributions to terrestrial ecosystems. A lower stream signature indicated that the subsidy between the stream–terrestrial boundaries was less important. Therefore, they suggested the "signature" approach may be broadly applicable for considering spatial dynamics across ecosystem boundaries and the importance of ecosystem boundaries.

If the importance of a given ecosystem boundary is relatively high, we should consider the importance of that boundary when considering ecosystem function and community dynamics rather than other boundaries. The criteria for considering a boundary will depend on the functions or species being considered. In addition, the properties and position of a boundary may change over time (Strayer et al., 2003); accordingly, temporal changes in the relative importance of ecosystem boundaries and changes in the connecting position between ecosystems should also be considered.

4 Ecosystem boundaries and conservation

Debates centered on reducing the number of ecosystem boundaries considered, which I propose here, will be important for conservation biology because cross-boundary linkages among ecosystems are important for the protection and restoration of impaired ecosystems (Wiens, 2009; Lamberti et al., 2010). Restoration of a critical habitat might require restoration of natural linkages across boundaries before ecosystem structure and function can return (Lamberti et al., 2010). A consideration of which ecosystem boundaries are important for particular habitats or endangered species would be useful in planning for the conservation of ecosystem functions and species populations.

5 Conclusions

Here, I introduced a graph theory that was developed from four-color theorem to estimate ecosystem boundaries. Using graph theory, we can classify the ecosystem boundaries. In addition, I have emphasized that we should reduce the number of ecosystem boundaries considered, with reference to the relative importance of each boundary. I have described the historical story of the four-color theorem in mathematics to suggest a way of considering boundaries on an ecological map. It is now time to reconsider ecosystem boundaries to move toward providing simplified theories of ecosystems, which have many boundaries, and to apply these theories to conservation biology and planning. For a simple mathematical map, 120 yr were needed to prove the “four-color issue”. How much time will we will need to prove the “four-color issue of ecology”?

Edited by: R. Brandl
Reviewed by: two anonymous referees

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