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# SUCCESSIONAL DYNAMICS OF SOIL MICROBIAL COMMUNITIES UNDER ANTHROPOGENIC IMPACT: APPROACHES TO MATHEMATICAL MODELING

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*У статті узагальнено сучасні наукові підходи до вивчення та моделювання сукцесії ґрунтових мікроорганізмів в антропогенних екосистемах, зокрема в українських агроценозах в умовах зміни клімату та воєнного впливу. Показано, що ґрунтова мікробіота є ключовим регулятором циклів карбону, азоту та інших елементів живлення, а сукцесійні зміни мікроорганізмів визначають родючість ґрунту, його стабільність і здатність до самовідновлення. Проаналізовано внесок провідних іноземних і українських учених у розроблення концепцій мікробної сукцесії, зокрема trait-based моделей, мікробно-орієнтованих моделей типу MIMICS, підходів, що враховують мікробну біомасу у процесах гумусоутворення, а також концепції функціональної сукцесії. Особливу увагу приділено впливу антропогенних чинників — інтенсивного землеробства, хімізації, змін землекористування, глобального потепління та воєнних дій — на траєкторію мікробної сукцесії. Показано, що забруднення ґрунтів важкими металами, вибуховими залишками, паливно-мастильними матеріалами спричиняє регресивну сукцесію, спрощення структури мікробіоценозу та порушення екосистемних функцій. Узагальнено результати досліджень українських учених щодо трансформації мікробних спільнот за різних систем землеробства, ролі мікроорганізмів у циклі азоту, фітопатогенних і антагоністичних грибів, а також можливостей керованої сукцесії через застосування біологічних препаратів. Розглянуто основні методи моделювання мікробної сукцесії: класичні математичні моделі (Моно, Лотки–Вольтерри, регресійні підходи), мережевий аналіз, стохастичні та нульові моделі асемблювання, а також сучасні методи машинного навчання (Random Forest, Gradient Boosting, нейронні мережі, MaxEnt). Обґрунтовано доцільність їх використання для прогнозування деградації та відновлення ґрунтів, оцінювання екологічного стану агроекосистем і розроблення практичних рекомендацій щодо рекультивації земель, уражених антропогенним і воєнним впливом. Отримані результати та узагальнені підходи до моделювання сукцесії ґрунтових мікроорганізмів сприятимуть глибшому розумінню механізмів функціонування ґрунтових екосистем за умов інтенсивного антропогенного та воєнного навантаження. Використання сучасних математичних і комп'ютерних моделей дасть змогу підвищити точність прогнозування змін мікробіоценозів, своєчасно ідентифікувати ризики деградації ґрунтів і науково обґрунтувати заходи щодо їх відновлення. У практичному вимірі це сприятиме розробленню екологічно безпечних технологій землеробства, оптимізації застосування біологічних препаратів, збереженню родючості ґрунтів і продовольчої безпеки України, а також формуванню наукових основ відновлення агроекосистем у районах, постраждалих від воєнних дій.*

***Ключові слова:** ґрунтова мікробіота, антропогенні екосистеми, агроценози, функціональні характеристики мікроорганізмів, біорізноманіття, зміна клімату, воєнне забруднення, відновлення ґрунтів, біоіндикація.*

## INTRODUCTION

In modern conditions, Ukraine faces large-scale problems of soil degradation and pollution caused by the accumulation of heavy metals, petroleum products, explosive residues, toxic compounds, and mechanical destruction of the soil cover as a result of military operations. Such impacts lead to changes in the structure of soil microorganisms, a decrease in biodiversity, and disruption of natural succession processes.

Modeling succession of soil microorganisms in anthropogenically polluted ecosystems is an important scientific approach to understanding the patterns of micro-biocenosis restoration, predicting changes in their quantitative and qualitative composition under the influence of various factors, and assessing the stability of ecosystems. The results obtained can be used to develop effective strategies for the recultivation and restoration of agrocenoses, as well as to minimize environmental risks in regions contaminated as a result of military operations.

**The purpose of this work** is to conduct a literature review of modern approaches to modeling succession of soil microorganisms in anthropogenically polluted ecosystems in order to assess the impact of major anthropogenic factors on the functioning of soil microbial communities.

## ANALYSIS OF RECENT RESEARCH AND PUBLICATIONS

A large number of foreign scientists [1–3] are engaged in the study of microbial succession in soils and the analysis of the biological, chemical, and physical characteristics of soil. International research often focuses on the development of complex microbially explicit models used to analyze the physiological properties of microorganisms to predict carbon and nutrient cycles.

William Withers [4] is one of the main developers of the MIMICS (MIcrobial-MIneral Carbon Stabilization) model (*Fig. 1*).

This model uses functional groups of microorganisms (copiotrophs and oligotrophs) to model the dynamics of soil organic carbon and its stabilization. This, in turn, affects the succession of microorganisms under conditions of anthropogenic impact and climate change. Wieder also analyzed how microbial communities change each other over the years and proved that soil carbon dynamics depend not only on climate, but also on how efficiently microbial communities convert plant residues into their own biomass (Microbial Growth Efficiency) [5].

Stuart Grandy and Cynthia Kellenbach collaborated with W. Wieder [6; 7] in the development and application of the MIMICS model. Their work focused on the role of microbial biomass and necromass in the formation of soil organic matter. Prior to the research of Kellenbach and Grunzi, it was believed that humus was mainly undigested plant residues. In their work, they proved that stable organic matter (SOM) in soil consists mainly of the«bodies» of dead microorganisms. During the decomposition of plant residues, some groups of microbes (fast colonizers) are replaced by others (more efficient ones). Each generation leaves behind necromass, which«sticks» to soil minerals, creating carbon reserves.

Scientists who have made a significant contribution to the study of microorganisms and their succession are Peter Van Bodeen

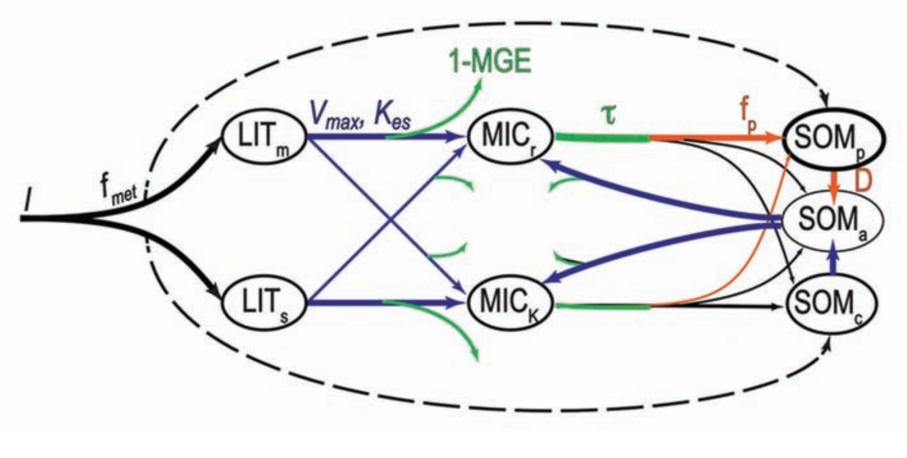


**Fig. 1.** MIMICS (MIcrobial-MIneral Carbon Stabilization) model (William Withers, 2015) [26]

and Ivan Janssens [8–10], who in their works reveal the essence of the integration of microbial functional traits into large-scale ecosystem models, as well as the response of the soil microbiome to anthropogenic influences and various types of changes in the environment. Van Bodegem was one of the first to use a«trait-based approach» to microbial communities [11]. His works explain why traditional succession is less important for the climate than functional succession, i.e., what microorganisms that replace each other do. He argues that it is not necessary to know the names of all bacteria to predict ecosystem processes. The most important thing is to know their strategies: growth rate, stress resistance (drought, temperature), and resource consumption to maintain life. In these studies, succession is viewed as a continuous process of filtering traits by the environment. For example, when land use changes, there is a succession shift towards microorganisms with higher«survival» costs, which in turn reduces the rate of organic decomposition.

Ivan Janssens [11] is one of the most cited ecologists in the world. His contribution concerns how anthropogenic factors (warming, nitrogen pollution) affect natural microbial succession. Janssens has shown that excess nitrogen, which is produced by fertilizer application or emissions into the environment, changes the trajectory of microbial succession in forest soils. Instead of active decomposers, groups that slowly decompose resistant organic matter (lignin) begin to dominate, leading to an unexpected accumulation of carbon in the soil. He used natural soil warming in Iceland to study how long-term warming changes microbial communities. His work proves that succession under warming conditions leads to the depletion of available carbon, after which microbiological activity drops sharply (the community adaptation effect).

Carlos Guerra and Manuel Delgado-Baquero [12; 13] analyze and predict the impact of climate change and anthropogenic influences on soil microorganisms, which is an important tool for understanding microbial succession. One of their most famous joint works is devoted to predicting how the soil microbiome will change by 2100. In this work, the process is viewed as a large-scale temporal succession caused by global changes.

They found that the succession path of many ecosystems leads to«uniformity.» Unique local communities are being replaced by a limited set of common microbial species. These scientists were able to prove that climate change is a more powerful driver of global«succession» than changes in land use (e.g., deforestation) [14].

Delgado-Bacuerizo [15] developed a concept highlighting that the composition of microbial communities (the result of succession) is more important for soil functions than simply the number of species. He showed that when external conditions change (e.g., increased aridity in deserts), microbial networks are restructured. This can be viewed as«regressive succession,» where complex networks of interactions break down, ultimately leading to a loss of the soil's ability to retain carbon and nitrogen.

Zhang Xia [16] is developing models of microbial decomposition of soil organic carbon that mimic the physiological transitions of microorganisms (active or dormant state) in response to changes in the environment that are characteristic of anthropogenic systems. One of Zhang Xia's most important recent works (co-authored with a group led by Zhang Kerong, published in Global Change Biology) is a large-scale meta-analysis of more than 5,000 soil samples from around the world. The researchers have shown [17; 18] that regardless of the type of ecosystem (forest, meadow, or primary succession after a glacier), microbial communities become more similar in composition over time (converge).

In the early stages, the dynamics are mainly determined by«species addition» (colonization). In later stages,«species replacement» (the displacement of some groups by others) dominates.

Zhang confirmed that during succession, the soil microbiome transitions from r-strategists (copiotrophs that grow rapidly on simple carbohydrates) to K-strategists (oligotrophs that slowly decompose stable organic matter).

In Ukraine, research in similar areas is traditionally conducted at the Institutes of the National Academy of Sciences of Ukraine (especially in the fields of soil science, microbiology, and agroecology), as well as at agricultural universities.

Beznosko's research [19] (in particular, within the framework of her work at the Institute of Agroecology and Nature Management of the National Academy of Agrarian Sciences) focuses on how anthropogenic pressure and different farming systems change the«microbial agrocenosis» of the soil. According to the author's work, a change in cultivation technology (from intensive to organic) significantly transforms the structure of the soil microbiota. The key group that responds to mineral fertilizers is nitrogen cycle microorganisms, namely ammonifiers and amylolytic microorganisms. Ammonifiers are bacteria that break down organic nitrogen compounds into ammonia. With intensive technologies, their numbers can grow, but an imbalance is often observed. Amylolytic microorganisms use mineral forms of nitrogen. Studies show that adding straw together with a compensatory dose of nitrogen stimulates this group, which promotes faster mineralization of plant residues.

As for the impact on ecological-trophic groups, the number of organotrophs, i.e., microorganisms that feed on organic matter, in organic farming systems (using manure and green manure) is significantly higher in terms of quantity and biodiversity compared to areas of intensive crop cultivation. Beznosko's studies often record changes in the pedotrophic coefficient, which indicates whether humus is accumulating or being«burned» by microorganisms.

Intensive technologies (excessive use of pesticides, monoculture) also lead to the accumulation of phytopathogenic fungi (e.g., *Fusarium* spp., *Alternaria* spp.). With environmentally safe technologies, the proportion of antagonistic fungi (e.g., fungi of the genus *Trichoderma* spp.) increases, which suppress plant diseases naturally.

Patika [20] is a leading expert in the field of soil microbiology and biologization of agriculture. Her work is devoted to the study of the functional stability of soil microbial complexes, the dynamics of microbial processes in agrocenoses, and the influence of biological products on microbial succession. The author actively researches changes in microbial communities in the root zone of plants (rhizosphere). He studies how the continuous cultivation of a single crop disrupts natural succession. The cultivation of only one crop leads to the accumulation of phytotoxic forms of microorganisms (for example, some species of fungi of the genus *Fusarium* spp.). Beneficial groups (nitrogen fixers, phosphate mobilizers) are also suppressed, leading to soil degradation. His work analyzes how different farming systems change the vector of microbial community development. Organic farming promotes the formation of succession with a predominance of microfungi and humus stabilization. With intensive technologies, when high doses of mineral fertilizers and pesticides are used, a«simplification» of succession is observed, in which biodiversity is reduced, leading to system instability.

A significant part of the work is devoted to the restoration of soils contaminated with heavy metals or pesticides [20; 21]. Patika investigates how the introduction of specific destructive strains triggers the process of secondary succession, in which the normal structure of the microbiocenosis is gradually restored after technogenic shock.

The study of the dynamics of soil microbial communities, their role in the transformation of nitrogen and phosphorus, as well as their response to various types of anthropogenic stress is characteristic of Nagorna's research [21].

Kovalenko and Kozyrev [22] are actively researching microbiological processes in the soils of Eastern Ukraine, in particular, the reaction of the microbial complex to the recultivation of disturbed lands and the formation of microbial succession in technogenic territories. One of the main aspects of their work is the study of the decomposition processes of stubble of such crops as wheat, corn, and sunflower. They are investigating how the introduction of biodestructors changes the sequence of microorganisms: from pioneer fungi to cellulolytic bacteria. The introduction of biodestructors accelerates mineralization and prevents the accumulation of pathogens. Optimizing this process allows nutrients to be returned to the soil more quickly, which is a form of controlled microbial succession.

These scientists also studied the effect of fertilizer irrigation on microbial communities. In the Southern Steppe region, irrigation radically changes environmental conditions. The works of Kovalenko and Kozyrev show how moisture changes the dominant ecological and trophic groups of microorganisms, and how mineral fertilizers can simplify the structure of microbial communities by suppressing beneficial microbiota (e.g., nitrogen fixers) and triggering succession processes that lead to humus degradation.

Important research has been done by Volokhon [23]. He is primarily known as a practicing microbiologist, and under his leadership, conceptual models for managing microbial processes have been developed at the Institute of Agricultural Microbiology (Chernihiv). In his work«Microbial Preparations in Agriculture. Theory and Practice,» he substantiates models of the influence of biological preparations on the direction of microbiological processes. He uses coefficients (for example, the mineralization-immobilization coefficient) that allow us to assess how the state of the soil will change when microbial succession changes under the influence of fertilizers.

Iutynska [24] is engaged in the development of various parameters for modeling the functional structure of the microbiocenosis. She proposed using the Shannon index and other mathematical indicators of biodiversity to model the stability (resistance) of soil systems to anthropogenic stress. Her models allow predicting whether the microbial community will return to its original state after stress.

Polupan [25], although better known as a soil scientist, laid the foundation for modeling soil ecogenesis, where microbial succession is the main driver. He developed models of humus formation in which microbiological activity acts as a key variable. Using this model allows us to predict the rate of carbon accumulation or loss in different climatic zones of Ukraine.

The study of soil microorganism succession is very relevant, given many aspects, especially the constant change in climate. Global warming and extreme droughts in recent years are significantly changing the trajectory of microbial succession. Rising temperatures accelerate the succession of r-strategists (bacteria that rapidly decompose organic matter). The acceleration of r-strategist succession leads to carbon that should have been stored in the soil for decades being rapidly released into the atmosphere in the form of carbon dioxide. Frequent fluctuations between drought and heavy rainfall deplete microbial communities. Succession simply does not have time to reach a stable stage (climax), leaving the soil biologically impoverished and vulnerable to erosion. Changes in climatic conditions have led to the appearance of microorganisms in Ukrainian agrocenoses that were previously characteristic of more southern latitudes. Thermophilic fungi and bacteria are beginning to dominate succession processes, causing new diseases in agricultural crops. New organisms can displace native species of nitrogen fixers or phosphate mobilizers. This destroys symbiotic relationships that have developed over centuries, causing cultivated plants to lose their natural immunity and require more chemical fertilizers and pesticides.

As for the impact of military operations, in Ukraine they have put unprecedented pressure on soil ecosystems. Contamination with heavy metals (lead, cadmium, mercury), explosive residues, and fuels and lubricants creates conditions for«regressive succession.» Explosives are toxic to most soil microbes. Succession stops or shifts toward the dominance of only those few species that can survive in conditions of chemical pollution. Shell craters mix the genetic horizons of the soil. Deep layers with dead microbiota end up on the surface, completely destroying the vertical succession structure of the microbiome.

If destructive bacteria disappear in succession, toxic compounds do not decompose. As a result, they enter plants and, subsequently, the human body along with food. Research on this topic is important now because without understanding how succession occurs in contaminated soil, it is impossible to calculate how many years it will take for black soil to recover on its own (it could be decades or even centuries). Knowledge of succession mechanisms allows scientists to transfer to contaminated soil precisely those microorganisms that will be the first to restore it and prepare the soil for the return of vegetation. Atypical species of microorganisms in agrocenoses are a direct threat to crop yields. Monitoring succession helps to identify the threat of new disease outbreaks in a timely manner. Microbial succession is the foundation of ecosystem restoration. The study of microbial succession is also important because of:

*Ecosystem functionality* — soil microorganisms (bacteria, fungi, archaea, algae) play a central role in the cycle of nutrients (nitrogen, phosphorus, sulfur), decomposition of organic matter, soil formation, and detoxification. Any change in the species composition and activity of microorganisms (i.e., in succession) directly affects soil fertility and plant nutrition.

*Resilience (resistance)* — succession changes show how well an ecosystem can withstand stressors (resistance) and recover from them (resilience). Anthropogenic ecosystems, such as agricultural fields, are less stable than natural ones, and studying succession helps to understand their adaptive capabilities.

The use of microorganisms as bioindicators is one of the most promising areas of agroecology. Since microbiota has high metabolic activity and rapid generational turnover, it responds to pollution or changes in agricultural technologies much faster than chemical indicators of soil or plant condition. The use of microorganisms as bioindicators is one of the most accurate ways to assess the state of an agroecosystem. Since microorganisms have a tremendous reproduction rate and direct contact with the environment, they respond to pollution much faster than plants or animals.

Soil microbiota acts as the«immune system» of the agrocenosis. Their response to stress (pesticides, heavy metals, salinization) manifests itself on three levels:

- *sensitivity* — even low concentrations of toxins alter the growth rate of bacteria;
- *functionality* — the intensity of soil respiration and enzymatic activity changes;
- *structure* — some species (sensitive) disappear and others (resistant) dominate.

Analysis of microbial composition allows you to:

- diagnose«soil fatigue» before crop yields begin to decline;
- assess the effectiveness of recultivation (whether life in the soil is restored after cleaning);
- adjust fertilizer application based on the actual state of the biota, not just chemical tests.

The work of contemporary Ukrainian scientist Simochko [26] is a significant contribution to understanding how fertilizers and anthropogenic pressure transform the microbial landscape. Microbial soil indication is based on the analysis of succession structure: the redistribution of populations indicates the extent to which the ecosystem is capable of self-recovery or the stage of degradation it is at. In his research, Simochko emphasizes that the application of different types of fertilizers (mineral versus organic) creates a specific«microbial response.» Intensive use of mineral fertilizers leads to an outbreak of bacteria that rapidly mineralize organic matter (copiotrophs), but at the same time inhibits the development of nitrogen-fixing bacteria and beneficial fungi. The change in the ratio between bacteria, actinomycetes, and fungi serves as a marker of soil«health.» For example, a sharp increase in the proportion of phytotoxic fungi of the genus *Fusarium* spp. or *Penicillium* spp. signals the degradation of the agrocenosis. Microbiologists use the following indicators to assess contaminated agroecosystems:

- *microbial biomass* — a sharp decrease in the total mass of microbes indicates toxic effects (heavy metals, pesticides);

- *microbial metabolic rate* — if microorganisms expend too much energy on respiration compared to biomass accumulation, this is a sign of ecosystem stress.
- *enzyme activity* — catalase and dehydrogenase are markers of metabolic intensity.

Successional changes as a marker of anthropogenic load are highlighted in the works of Simochko and other microbiologists [26], which reveal the concept of«adaptive restructuring» of the microbiocenosis. When a pollutant enters the agroecosystem, succession changes its natural course. At the elimination stage, sensitive species (symbiotes, specialized destructors) die out. At the stage of dominance of resistant forms, microorganisms that are able to use the pollutant as a food source or are resistant to it multiply. At the simplification stage, a«poor» community with low biodiversity is formed, which is unable to perform all ecosystem functions (for example, the nitrogen cycle is interrupted).

A large number of methods and models can be used to study and model microbial succession, depending on the research task, available data, and desired results. Trait-based models are the most relevant approach for anthropogenic systems (*Fig. 2*) because they model not specific species but their survival strategies (e.g., the MIMICS model).

This model is based on the division of microorganisms into groups: copiotrophs

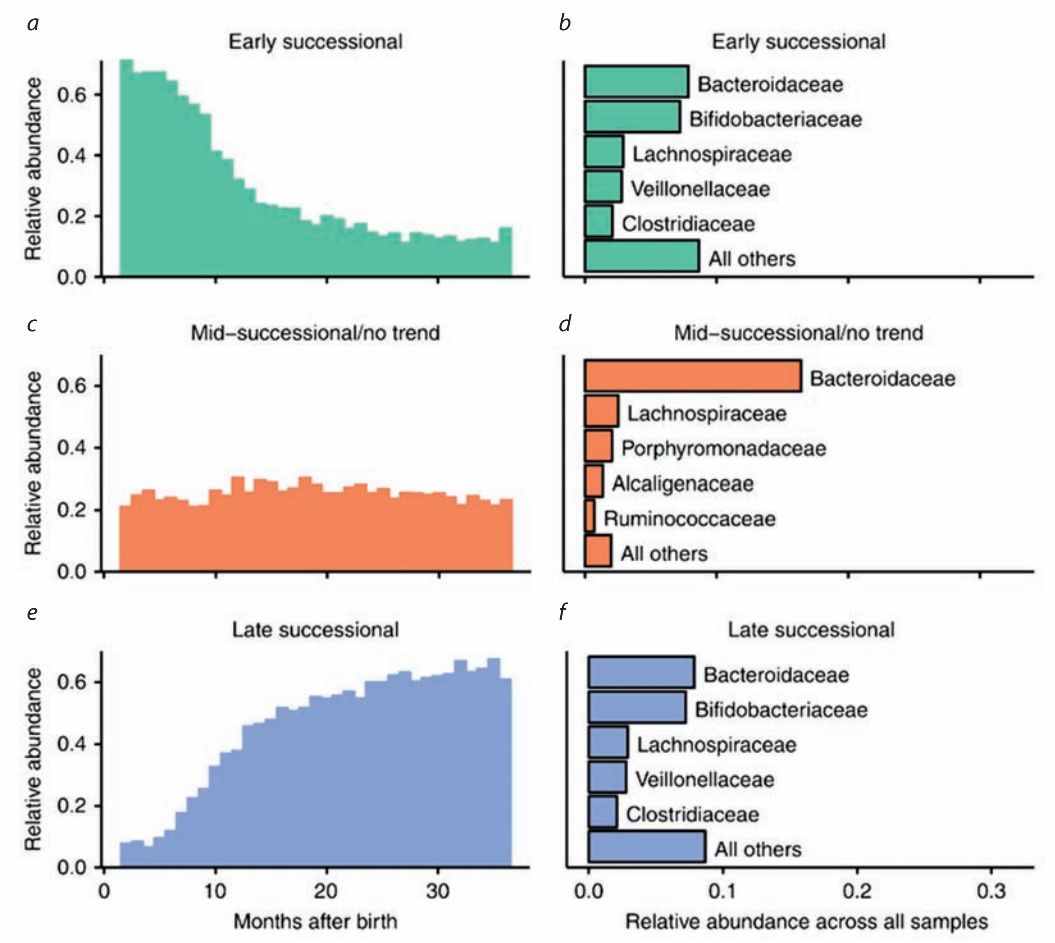


**Fig. 2.** Trait-based models [27]

(r-strategists that grow rapidly on fertilizers) and oligotrophs (K-strategists that survive in poor soils). These models allow us to predict how the application of high doses of nitrogen fertilizers will shift succession towards humus mineralization.

Mathematical modeling of population dynamics (Lotka-Volterra & Monod) is also common. These are classic methods used to describe interactions between groups of microorganisms in a contaminated environment. The Monod equation describes the growth rate of microbes depending on the concentration of the substrate (e.g., oil pollution or pesticides). Lotka-Volterra models are used to model competition between«native» species and invasive (atypical) species that have appeared due to climate change. The main application of these methods is to calculate the time it takes for beneficial microbiota to displace pathogenic microbiota after the introduction of biological products.

Network analysis is also widely used to model the succession of microorganisms. This method allows us to model not only the number of microorganisms, but also the strength of the connections between them. Interaction networks are constructed based on DNA sequencing data. In anthropogenic systems, these networks often become«fragile.» This method can be used to model the impact of military pollution. If the network breaks down into separate modules, this predicts complete degradation of the ecosystem.

Stochastic and deterministic assembly models help to understand whether the change in the microbiome is random or regular. One example of these models is zero models (*Fig. 3*), which allow us to assess the extent to which succession after military shock is determined by the random introduction of new species (dispersal) and the extent to which it is determined by environmental selection.

These models can be used to assess the self-recovery potential of soil. If«randomness» dominates succession, the soil needs artificial introduction of microorganisms (inoculation).

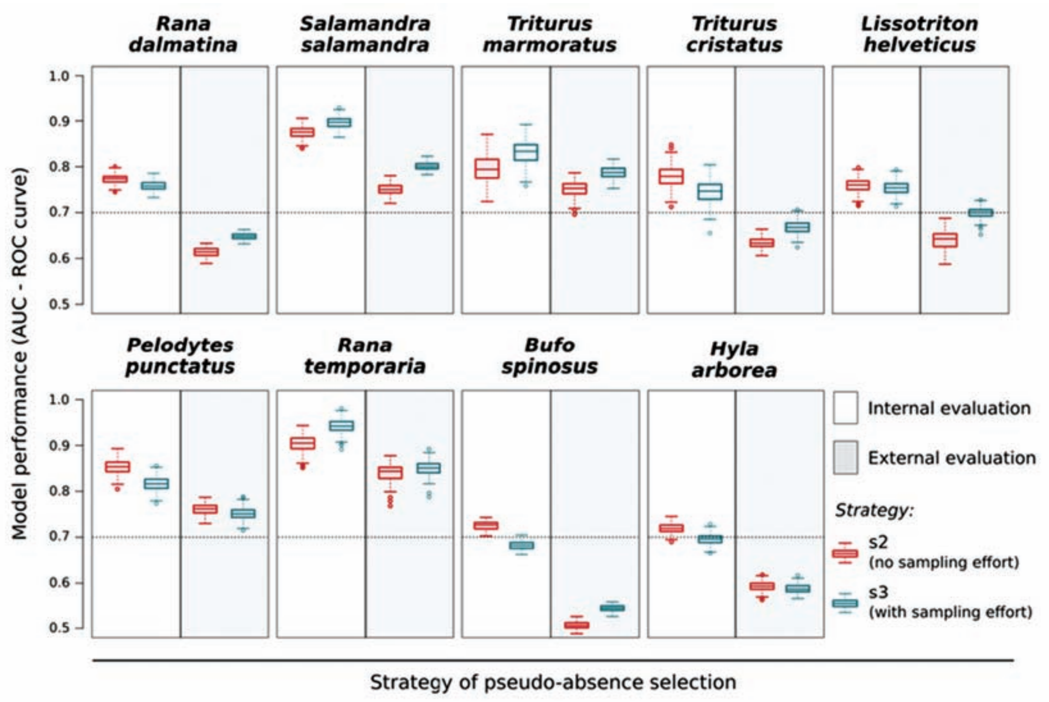


**Fig. 3.** Null models for assessing new species [28]

A modern method for modeling is machine learning models. Machine learning methods (*Fig. 4*) allow determining the stage of restoration or degradation of the soil by analyzing its«microbial fingerprint."

The most popular model in soil biology is Random Forest (*Fig. 4, a*). It allows determining«indicator taxa» — microorganisms that most strongly indicate the age of succession or the level of pollution. Gradient Boosting models (XGBoost, CatBoost) (*Fig. 4, b*) are used to predict how quickly a community will change under the influence of climate. These models are very accurate in conditions where the data has complex nonlinear relationships.

In the context of climate change, it is important to know which new species (including pathogens) will appear in agrocenoses. MaxEnt (Maximum Entropy Modeling) — this

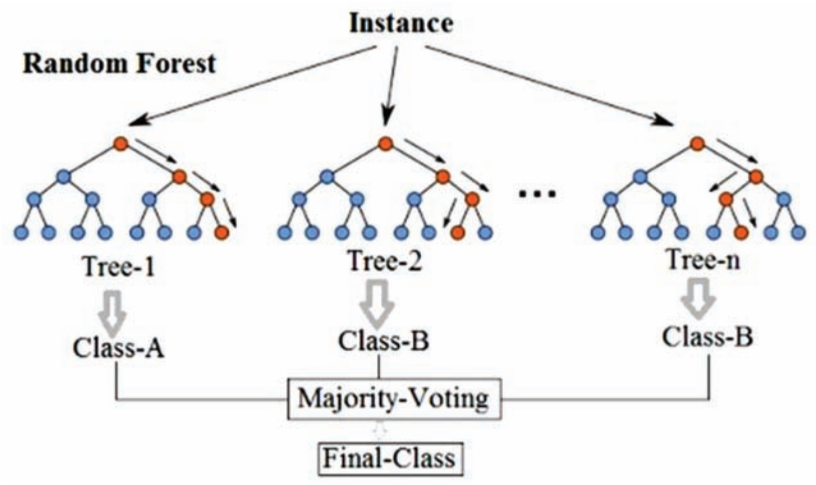


**Fig. 4, *a*.** Random Forest model [29]


**Fig. 4, *b*.** XGBoost model [30]

model has traditionally been used for macroecology, but has now been adapted for microorganisms. The model predicts the probability of a species appearing at a specific geographical point based on climate data.

Artificial neural networks (ANN) can model complex ecological niches, predicting how a 1.5°C warming will change the ratio of bacteria and fungi in succession.

The classic method for modeling microbial succession is multiple linear regression (MLR). It can be used to establish a relationship between time (succession stage) and physicochemical soil parameters (acidity level, nitrogen content, temperature). Using a linear multiple regression model, it is possible to predict the total microbial biomass depending on the content of heavy metals and organic carbon. The research data are presented in the works of scientists such as Iutynska and Simochko for toxicity assessment.

Nonlinear and polynomial regression are also actively used. Succession is not always linear. In the early stages after contamination (e.g., military), there is a sharp decline in biodiversity, followed by a slow recovery. Therefore, in such cases, it is advisable to use these models to simulate succession.

Thus, in connection with the war, which causes constant chemical and physical contamination of soils, destruction of its layers, deterioration of the physiological properties of the soil, as well as due to the negative impact of economic activity, there is an acute issue of restoring and preserving the physiological properties of soils and their fertility. It is important to predict stable and safe conditions for growing crops. Mathematical models make it possible to develop a set of methods for assessing the ecological state of agroecosystems affected by economic activity, especially military action. They also make it possible to predict the future state of ecosystems, identify factors that influence their restoration, and develop recommendations for restoring soil ecosystems. The ecological and economic effect of implementing these models includes restoring agrocenoses with the help of microorganisms, reducing the harmful impact of various types of pollution on the environment, and restoring the physiological properties and fertility of soils.

## CONCLUSION

The analysis of the literature shows that the succession of soil microorganisms is a fundamental mechanism for the functioning and restoration of anthropogenic ecosystems, since it is the microbiota that determines the intensity of nutrient cycling, the stabilization of organic carbon, the resistance of soils to stress, and their fertility. Under conditions of increased anthropogenic pressure, climate change, and military action, microbial succession often becomes regressive, leading to a simplification of the structure of microbiocenoses, disruption of ecosystem functions, and soil degradation. That is why the study and modeling of these processes are extremely important, as they allow not only to objectively assess the ecological state of soils and predict their future changes, but also to scientifically substantiate effective measures for recultivation, biologization of agriculture, and controlled restoration of agroecosystems. The use of modern mathematical, network, and machine models allows us to move from describing the consequences of degradation to actively managing microbial processes, which is critically important for preserving soil fertility, the ecological stability of agricultural landscapes, and food security in Ukraine, especially in areas affected by war.

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