

The microbiome of peatland plants – literature review

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Abstract: The aggregate of various taxonomic groups of microorganisms colonising living organisms is known as the microbiome. The plant microbiome encompasses a wide network of biological, chemical and metabolic interactions between the plant and microorganisms (mainly algae, bacteria and protozoa). The relationships between microbes and peatland plants, particularly carnivorous plants, are a very interesting subject that is still little understood. Microbes colonising carnivorous peatland plants may be present in their traps or on the surface of the plant. Previous research on the relationships between the microbiome composition of carnivorous plants and the external factors influencing it directly and indirectly is still inadequate. There is a lack of review articles analysing the current state of knowledge regarding carnivorous plant–microbiome interactions. This review of the literature is a collection of data on the functioning of the microbiome of carnivorous plants growing in peatland ecosystems. In addition, it summarises the available information on host–microorganism relationships.

Keywords: carnivorous plants, ecosystem, microbiota, microorganisms, peatbog plants, peatland, wetlands

INTRODUCTION

Peatlands accumulate large amounts of biogenic elements of sedimentary origin (Flessa *et al.*, 2002). The decomposition process results in the formation of organic matter and deposits of peat (Flessa *et al.*, 2002; Robson *et al.*, 2005). Unfortunately, due to global climate change and drainage of peatlands, peat-formation processes are increasingly vanishing, which has been observed over 20% of the global area of peatlands (Parish *et al.* (eds.), 2008). Bradshaw (1983) stated on the degradation of the vast majority of peatlands in developed countries and its negative consequences for the functioning of nature (Bradshaw, 1983).

The origin of peatland water, the moisture level of the environment, and eutrophication processes are the major factors influencing the occurrence of various groups of organisms in this ecosystem (Brix and Sorrell, 1996).

Peatlands are among the most important natural ecosystems for the preservation of biodiversity and regulation of the circulation of matter in the biosphere (Parish *et al.*, 2008; Mitsch and Gosselink, 2009). Primary production of organic matter in plant communities far exceeds its decomposition. As a result of this process, there is an accumulation of layers of peat soil (Amesbury, 2016). Dissolved organic matter is a mosaic of

various chemical elements and is included in the classical grazing food chain. Released by primary producers, it migrates through successive levels of the food web, influencing the model of carbon flow pathway and the nutrient cycle (Azam, 1998). The presence of *Sphagnum* moss is a beneficial factor for binding and accumulation of atmospheric carbon, through long-term accumulation of organic sediment composed of dead plant parts. It acidifies marshes and supports synthesis of compounds inhibiting the rate of *Sphagnum* decomposition, resulting in increased accumulation of biomass impeding the flow of minerals (Rydin and Jeglum, 2013). Peatland vegetation is associated with microbes by direct and indirect mechanisms (Mieczan and Bartkowska, 2022). The aggregate of various taxonomic groups of microbes colonising living organisms is known as the microbiome. The plant microbiome is a wide and as yet little understood network of biological, chemical and metabolic interactions between the plant and microorganisms (Freedman, 2021). While analysing the relationships between carnivorous plants and the microbes colonising their surface, we attempted to summarise previous research on this issue. The aim of this review was to present the available data on the functioning of the microbiome of peatland plants, with particular focus on carnivorous plants. We also focused on analysis of the effect of

selected physical and chemical parameters of the water and global climate change on the species richness and abundance of the microbiome of carnivorous plants.

MATERIALS AND METHODS

To summarise research conducted to date on the microbiome of peatland plants, with particular focus on carnivorous plants, an exhaustive review of the literature was conducted, covering the period from 1996 to 2022. Relevant scientific articles were identified by a systematic search of various online databases (Elsevier, PSJD, HighWire Press), most recently on 24 January 2023. The search strategy took into account keywords associated with hydrobiology and microbiomes. Google Scholar, PubMed and Scopus were searched using the following search words: “peatbog”, “microbiome”, “microbiota”, “peatbog plants”, and “carnivorous plants”. In addition, reference lists of review and research articles were manually searched for additional data. Main methodology for the selection of work based on analyse all available original articles associated with the microbiome of carnivorous plants. The works analysed were peer-reviewed and published in English. In total 77 articles associated with the microbiome of peatland plants were analysed.

RESULTS AND DISCUSSION

EFFECT OF HABITAT CONDITIONS ON PEATLAND PLANTS

Peatlands are habitats for many rare and distinctive plant species (Diggelen van *et al.*, 2006). Limited access to certain nutrients reduces the productivity of plants and leads to the evolutionary development of adaptive mechanisms to compensate for the deficiencies, including predation (Güsewell and Edwards, 1999). In well-functioning peatland ecosystems, a high groundwater level in the soil leads to anaerobic conditions, which reduces the redox potential of the substrate (Mars de and Wassen, 1999). Its value influences the degree of oxidation of micro- and macro-elements such as nitrogen, iron, or sulphur. Microbes closely associated with peatland vegetation (including carnivorous plants) are capable of reducing nitrate ions, trivalent iron ions, and sulphate ions in conditions of low potential. Increased redox potential results in oxidation of these compounds to forms easily dissolved in water (Zak *et al.*, 2010).

The availability of biogenic elements in the environment is a variable parameter. When they are deficient, the plant enters into a state of limited biomass production, resulting in inhibition of synthesis of above-ground organic matter (Boeye, Haesebroeck van and Verheyen, 2009). As access to at least one of the biogenic elements is always limited in peatlands, the productivity of plants present in these habitats is reduced (Chróst *et al.*, 2009). Furthermore, varying adaptations of plants to life in conditions such as low substrate fertility affects interspecific competition, mainly for nutrients (Kotowski and Diggelen van, 2004).

Content of mineral salts, moisture levels, and trophy are basic environmental parameters which are highly variable in peatland ecosystems. The species composition of the biocoenoses taken over by peatland plants depends in part on the ecological factors determining these environmental gradients (Rydin,

Jeglum and Hooijer, 2006). The specific habitat conditions have led to the emergence of a group of plant or animal species referred to as having narrow ecological amplitudes. Nutrients that are deficient relative to other elements will have a limited influence on them. In these wetland ecosystems primary production can be reduced by a deficiency of nitrogen, phosphorus, or potassium (Olde Venterink *et al.*, 2003). Physiological and morphological adaptations of peatland plants facilitate the acquisition and accumulation of elements. The structure of the root system, the type of limitation, and the mycorrhiza exert a significant influence on the species composition of the phytocoenosis (Lambers, 2006; Cameron *et al.*, 2007).

The optimum range of plant productivity maintaining biodiversity is narrow in phosphorus-deficient peatlands, and even a relatively small change in the P concentration can have a pronounced effect on the number of plant species present. As a biogenic element that takes on insoluble forms, phosphorus can also become a factor with limited availability (Pawlikowski *et al.*, 2003). Calcium and magnesium ions regulate the availability of phosphorus, calcium inactivates Fe in a form with low availability for plants, and iron supports migration of molecules and increases the percentage content of other elements (Pawlikowski *et al.*, 2003). The nitrogen concentration in peat is relatively high, but it is not always available to plants. Its content depends on the rate of mineralisation of dead organic matter and therefore fluctuates (Phoenix *et al.*, 2006). Limited access to nitrogen in the environment inhibits the growth of most plants. Only carnivorous plants or those living in symbiosis with nitrifying bacteria can function well in such extreme conditions (Cronk and Fennessey, 2001).

All carnivorous plants associated with peatland ecosystems are very often present in an environment with a high moisture level but low concentrations of nutrients (Adamec, 1997; Mieczan *et al.*, 2015). The survival of carnivorous plants in these conditions is possible owing to the benefits of their means of acquiring food (predation) (Giang, 2015). Nearly 500 vascular plant species are able to capture and digest small organisms in order to obtain nutrients (Barthlotta, 2004). *Lentibulariaceae*, the largest monophyletic family of carnivorous plants, includes three genera, *Pinguicula*, *Utricularia* and *Genlisea*, distinguished by their trap mechanisms (Adlassnig *et al.*, 2010; Giang *et al.*, 2015). Carnivorous plants also include *Aldrovanda vesiculosa* L. and *Sarracenia purpurea* L. Aquatic species of carnivorous plants are mainly present in environments poor in available minerals, which they take up through their shoots from the environment or from the bodies of their prey (Sirová *et al.*, 2010). Carnivorous plants attract and capture prey using various types of traps, usually each located on a separate leaf (Płachno, Adamec and Kamińska, 2015). Plants of the genus *Pinguicula* secrete sticky mucus to capture insects. Plants of the genera *Utricularia* and *Genlisea* use modified leaves as suction traps (*Utricularia*) or mosquito traps (*Genlisea*) (Giang, 2015). A key endogenous factor preventing the formation of traps is the nitrogen concentration in the stem. This regulation is a feedback loop – a decline in the nitrogen content in the stem stimulates trap formation, which enables the capture of more prey (Adamec, 2008).

When the prey touches the trigger hairs located on the trap, the trap opens and closes again after the prey is drawn inside (Sydenham and Findlay, 1973). The trap hairs, directed inwards, prevent the prey from escaping, allowing it to move only deeper

into the trap (Giang, 2015). The trapped organism is digested by the plant's digestive enzymes (Peroutka *et al.*, 2008). The digestive fluid of the trap leaves is acidic, due to the secretion of protons by epidermal cells. Acidity positively influences the action of enzymes and therefore the acquisition of nutrients by the plant (Adlassnig, Peroutka and Lendl, 2011). Digestion of organisms of smaller size or with thinner shells is more efficient than in the case of larger organisms (Adamec, 1997). This is confirmed by research conducted to determine the ability of trap leaves of *Drosera capensis* and *D. capillaris* to absorb elements such as nitrogen, phosphorus, potassium and magnesium from the body of insects (Adamec and Kondo, 2002; Płachno, Adamec and Huet, 2009).

The epidermis of the trap absorbs nutrients through its pores. Specialised trap leaves allow for increased absorption of macro- and microelements (Adamec, 1997). A significant modification of the means of obtaining elements may also be found in the root system. Some carnivorous plants, e.g. of the genus *Utricularia*, have no roots or produce them only for a certain period of the year (*Drosera* L.) (Adlassnig *et al.*, 2005). Instead of a root system, plants such as *Utricularia* have modified shoots without pigment, which take up minerals by penetrating the substrate (Adlassnig *et al.*, 2005). This reduction of the root system positively influences the intensive development of trap leaves (Adlassnig *et al.*, 2005; Sirová *et al.*, 2010). Some species of the genus *Genlisea* have developed underground traps for capturing protozoa and small Metazoa (Giang, 2015).

THE MICROBIOME OF CARNIVOROUS PEATLAND PLANTS

The processes defining the development of the microbial community associated with a host are not well known (Alkhalaf, Hübener and Porembski, 2009). Plant tissue can provide stable conditions for the development of microorganisms, so carnivorous plants are good substrates for the functioning of complex food webs and microbial communities (Ellison *et al.*, 2021). However, little is known of the interactions between the host and microbiome, apart from the role of microbes as a source of nutrients, and of the potential effects of the presence of microbes in the traps of carnivorous plants. Soil microorganisms associated with the root system or living inside plants have been shown to play an important role in the functioning of plants (Giang, 2015). Microbes associated with plants are recognised as key partners increasing uptake of macro- and microelements, alleviating stress in plants, stimulating growth, and facilitating effective defence mechanisms against pathogens (Rinke *et al.*, 2013; Berg *et al.*, 2014). Microbial communities associated with carnivorous plants play a major role in the detritus chain and C cycle (Mieczan and Bartkowska, 2022).

Experimental research carried out by Siragusa *et al.* (2007) showed that microbes can survive and multiply in many carnivorous plant traps. Within the traps of plants of the genera *Utricularia*, *Sarracenia* and *Genlisea*, diverse microbial communities, consisting mainly of bacteria, algae, protozoa, and rotifers, can support digestion of prey or themselves eventually become digested – Figure 1 (Giang, 2015; Siragusa, Swenson and Casamatta, 2007).

Sarracenia purpurea also uses carnivory to make up mineral deficiencies. The traps open to fill with rainwater and then attract insects, which drown in them (Grotjahn and Younge, 2015). The

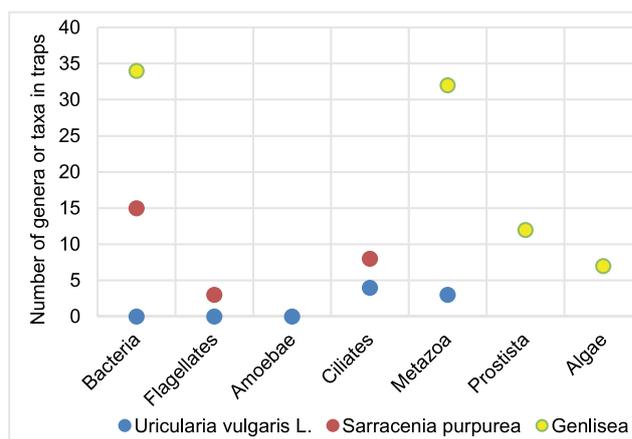


Fig. 1. Changes in number of different taxonomic groups in carnivorous plants; source: own elaboration based on: Giang (2015), Grotjahn and Young (2015), and Mieczan and Bartkowska (2022)

organisms are decomposed by invertebrates colonising *S. purpurea* (Newell and Nastase, 1998; Peterson *et al.*, 2008). Previous research on the food web provides important information, but knowledge is still lacking on other microorganisms colonising carnivorous plants such as *S. purpurea* and on the relationship between the diversity of eukaryotic organisms and the bacteria present in their leaf rosettes (Mouquet, Moore and Loreau, 2002; Gotelli and Ellison, 2006). The composition of microbes colonising these plants is known to differ between plant populations (Mouquet, Moore and Loreau, 2002; Peterson *et al.*, 2008). Research by Peterson *et al.* (2008), Koopman *et al.* (2012), Gray *et al.* (2012) and Canter *et al.* (2018) indicate the dominance of Proteobacteria, and Bacteroidetes and Firmicutes have been observed as well. The microbiome of *S. purpurea* may also contain autotrophic algae (Mouquet, Moore and Loreau, 2002; Gebühr *et al.*, 2006; Gotelli and Ellison, 2006; Koopman *et al.*, 2010; Gray, 2012; Canter *et al.*, 2018).

Carnivorous plants of the genus *Utricularia* are also colonised by various groups of microorganisms (Sirová, Adamec and Vrba, 2003). This is the largest and most cosmopolitan genus of carnivorous plant, with numerous traps (colonised by microbes) filled with bladder fluid and closed by mobile trap doors with sensory hairs (Rinke *et al.*, 2013). The effect of predation on the growth of *Utricularia* is dubious, especially in the case of species growing in nutrient-poor conditions (Friday, 1989). Despite their small volume, *Utricularia* trap fluid is permanently colonised by microorganisms, which enter the traps from the environment and can then multiply in them (at the same time obtaining nutrients during the digestion process) (Alkhalaf, Hübener and Porembski, 2009). Diverse microbial communities consisting mainly of bacteria, algae, protozoa and rotifers can live as epiphytes or parasites within *Utricularia* traps. They can also support the condition of plants in the context of digestion of their prey, before they are digested themselves (Sirová, Adamec and Vrba, 2003; Płachno, Adamec and Huet, 2009; Sirová *et al.*, 2010). Bacteria and algae have also been shown to occur in traps and to multiply in them (Richards, 2001; Sirová, Adamec and Vrba, 2003). Research by Płachno *et al.* (2012) indicates that both bacteria and flagellates are relatively stable elements of the microbiome of plants of the genus *Utricularia*. Bacteria in particular play a key role in the circulation of matter and energy within the traps of carnivorous plants (Płachno *et al.*, 2012). Some

traps capture prey and digest it, but all are colonised by microbes which start the activity of these structures (Richards, 2001). Research by Krasuska, Glinka and Gniazdowska (2012) and Sirova *et al.* (2018) indicates that the microbiome should reflect the main source of nutrients. There is a significant relationship between the anatomy of the walls of traps and their functional traits (Sirova *et al.*, 2011; Krasuska, Glinka and Gniazdowska, 2012). The more cell layers are present in the walls of traps, the less effective they are at processes such as water transpiration and pumping. Plants of the genus *Utricularia* enable the development of a variety of microbial communities, both within traps and on their outer surfaces, which allows for a higher rate of utilisation of accumulated organic matter. Due to the high respiration rate of both plant tissues and microbes, traps are characterised by anoxic conditions at night or during intensive digestion of organic matter. Short-term inflow of oxygenated water improves the oxygenation level each time the trap shows activity. This indicates that the interaction between the host plant and its microbiota involves mutual “cooperation” (Sirova *et al.*, 2011).

Previous research on the microbiome thus presents two main aspects: functional characteristics of the interaction between its traits and the host, and the effect of environmental factors on its functioning. However, microbial communities can exhibit varied sensitivity and stronger or weaker reactions to changes in environmental conditions (Mieczan and Bartkowska, 2022).

EFFECTS OF TEMPERATURE ON THE MICROBIOME OF PEATLAND PLANTS

Bacteria, algae, cyanobacteria, and ciliates were present in the traps of carnivorous plants. Interactions between carnivorous peatland plants and microorganisms are affected by temperature changes, because microbes are highly sensitive to this parameter (Adamek, 2011; Płachno *et al.*, 2012; Sirova *et al.*, 2018; Basińska *et al.*, 2022). Mieczan and Bartkowska (2022), in an experimental study, compared the effects of temperature changes on microorganisms present in the aquatic environment and in the traps of carnivorous plants. Effect of temperature on abundance, biomass and diversity of microorganisms was significant – Figure 2 (Mieczan and Bartkowska, 2022).

The abundance of flagellates in the aquatic environment was higher than in the traps. Irrespective of the habitat, the abundance of microbes increased in direct proportion to the temperature.

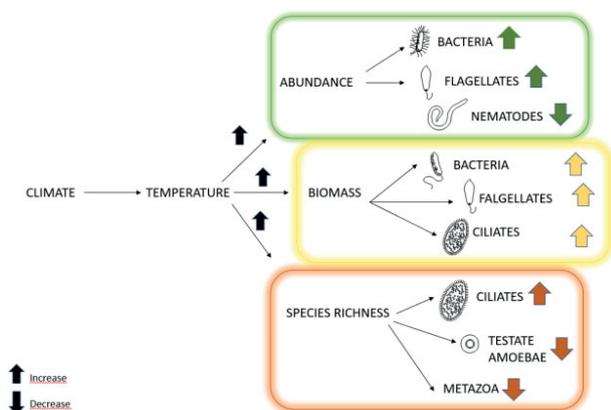


Fig. 2. The effect of temperature on the microbiome of carnivorous plants traps; source: Mieczan and Bartkowska (2022)

A similar relationship was observed for testate amoebae, which were also more abundant in the aquatic environment than in the traps of carnivorous plants. The abundance of testate amoebae decreased with increasing temperature. The dominant species in the aquatic habitat were *Arcella discoidea* and *Hyalosphenia elegans*, while only *Arcella discoidea* was present in the traps. The biomass of amoebae, on the other hand, was comparable in the two environments, and no significant effect of temperature on this parameter was observed (Mieczan and Bartkowska, 2022). In the case of ciliates, species richness increased with increasing temperature. In the aquatic environment there were 12–19 taxa (with dominance of *Paramecium bursaria*, *Urocentrum turbo* and *Litonotus lamella*), while 4 ciliate taxa were detected in the traps (with dominance of *Paramecium bursaria*). As in the case of amoebae, abundance of ciliates was higher in the water than in the traps of carnivorous plants. Irrespective of the environment, however, as the temperature increased there was an increase in the biomass of these organisms. The effect of climate warming on small Metazoa, including nematodes, was also investigated in the experiment. As the temperature increased, there was a decrease in the species richness of this group, as well as in biomass and abundance (in both the aquatic environment and the traps). The successive temperature increase (to max. 21°C) eliminated nematodes from the traps, while rotifers *Bdelloidea* and *Lecane* spp. began to dominate in the water (Mieczan and Bartkowska, 2022). Mieczan and Bartkowska (2022) showed a significant difference in the biomass of microorganism in the microbiome of carnivorous plants (in different temperature: 19°C or 21°C) – Figure 3.

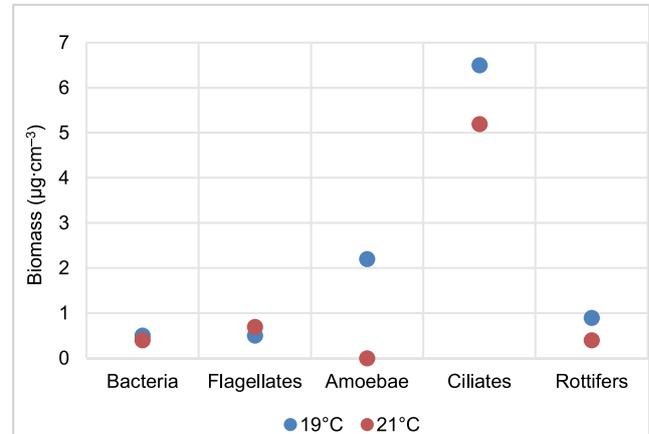


Fig. 3. The effect of temperature on the biomass of microbial and metazoan communities in *Utricularia*; source: own elaboration based on: Adlassnig *et al.* (2011) and Mieczan and Bartkowska (2022)

Increasing temperature affects the carbon storage process in the soil and vegetation, and sequestration may be impaired by the increased decomposition rate. This will increase the rate of release of nutrients from the environment (Hobbie, 1996; Mieczan and Bartkowska, 2022). Elevated concentrations of macro- and microelements caused by the rise in temperature most often increase the rate of microbiological production, including microbiome abundance (Mieczan and Bartkowska, 2022).

A study by Buosi *et al.* (2011) showed that as temperature increases there is an increase in the abundance of bacteria, with higher abundance in the water than in traps. On the other hand, a temperature increase was not shown to significantly affect the

abundance of ciliates in the microbiome of carnivorous plants (Buosi, 2011; Mieczan *et al.*, 2015).

Experimental research on the microbiome of *S. purpurea*, carried out by Freedman *et al.* (2021), showed that climate warming directly affects the taxonomic diversity of bacteria in traps. The same authors stated that the *S. purpurea* microbiome at all sites was dominated by Proteobacteria, Bacteroidetes and Actinobacteria. The taxonomic diversity of bacteria in traps increased with the temperature.

Therefore, an increase in water temperature significantly modifies the qualitative and quantitative structure of communities of microbes and small Metazoa, and thus the microbiome of carnivorous plant traps (Tab. 1, Fig. 4).

they continue to take up nutrients (Giang *et al.*, 2015). Traps at different stages of development most likely have the capacity for functional changes. Some carnivorous plant species can produce hydrolases continuously. Adamec *et al.* (2010) demonstrated low activity of aminopeptidases in trap fluid (Adamec *et al.*, 2010). This may be largely due to penetration of aminopeptidases with low activity from the surrounding water. Information on enzymatic activity in filtered trap fluid remains scarce. It is also not known whether the trap glands of carnivorous plants or the commensal organisms colonising the plants significantly influence the activity of these enzymes (Sirová *et al.*, 2010).

Microbes colonising carnivorous peatland plants can be present in the traps or on the plant's surface. Studies have shown

Table 1. Dominance structure of microorganism in the microbiome of carnivorous plants

Plant	Dominance taxonomic group			
	<i>Amoebae</i>	<i>Ciliata</i>	<i>Bacteria</i>	reference
<i>Utricularia vulgaris</i> L.	<i>Hyalosperia elegans</i> , <i>Arcella discordes</i>	<i>Parmecium bursaria</i>	n.d.	Mieczan and Bartkowska (2022)
<i>Sarracenia purpurea</i> L.	n.d.	<i>Scuticociliatia</i> , <i>Orchitophyridae</i>	<i>Coxiellaceae</i> , <i>Saccharibacteria</i>	Grotjahn and Young (2019)
<i>Genlisea nigrocaulis</i> Steyerl.	<i>Phalansterium</i> , <i>Paradermamoeba</i>	<i>Tetrahymena</i>	<i>Entophlyctis</i>	Giang <i>et al.</i> (2015)
<i>Sarracenia purpurea</i> L.	n.d.	n.d.	<i>Proteobacteria</i> , <i>Bacteroidetes</i> , <i>Actinobacteria</i>	Freedman <i>et al.</i> (2021)

Explanations: n.d. = no data available.

Source: own results.

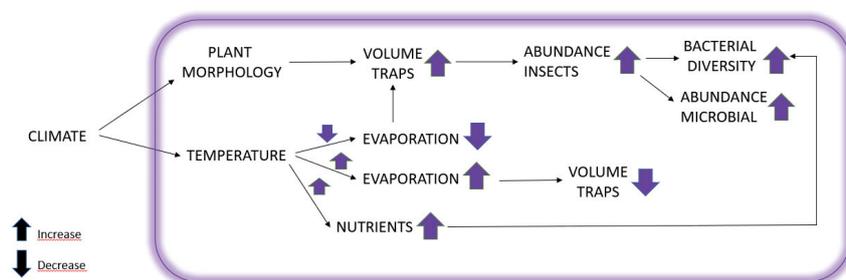


Fig. 4. The effect of climate on the plant morphology traps; source: own elaboration based on: Grotjahn and Young (2019), Freedman *et al.* (2021), Ellison (2021), and Grotjahn and Young (2022)

EFFECTS OF NUTRIENTS ON THE MICROBIOME OF PEATLAND PLANTS

There is little information concerning host–microbiome interactions, and it mainly indicates the important role of microbes as a source of nutrients – for carnivorous plants (Giang *et al.*, 2015). Biochemical analyses have detected proteases, phosphatases, and esterases in fluid collected from *Utricularia* traps (Giang *et al.*, 2015). Phosphatase showed the strongest activity, while that of the other enzymes was weaker. Giang *et al.* (2015) determined the activity of proteases, chitinases and phosphatases produced by *S. purpurea*. These enzymes exhibited the highest activity within the first few weeks after the traps became active. When *S. purpurea* ages, its activation energy declines, and thus its enzyme activity declines. Old traps stop producing digestive enzymes, but

higher nutrient concentrations in traps without prey than in those with a captured organism (Sirová *et al.*, 2010). Adllasnig *et al.* (2012) showed that carnivorous plants of the genus *Utricularia* take up nutrients by endocytosis, while plants of the genus *Sarracenia* take up nutrients by carrier proteins – Figure 5 (Adllasnig *et al.*, 2012).

Carnivorous peatland plants take part in the organic carbon cycle. However, due to the high rate of photosynthesis, the effects of this energy expenditure are negligible for the plant (Sirová *et al.*, 2009; Sirová *et al.*, 2010). Analysis of trap fluid also indicates high concentrations of simple sugars and organic acids, which also promotes microbial development (Sirová *et al.*, 2010). The endosymbiotic relationship between ciliates and algae of the genus *Zoochlorella* indicates partial autotrophy. Therefore, the microbiome of *Utricularia* traps seems to be dominated by eukaryotes containing symbionts, which can significantly increase

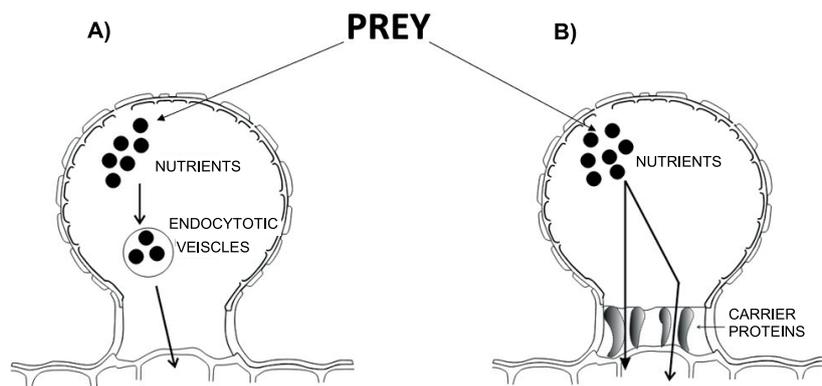


Fig. 5. Uptake via endocytosis – *Utricularia* (A) and transport of the peptides via specific carriers – *Sarracenia* (B); source: own elaboration based on: Adllasnig *et al.* (2012)

primary production, constitute a source of dissolved organic carbon, and provide nutrients to the plant (Sirová *et al.*, 2018; Mieczan and Bartkowska, 2022).

THE AGE OF TRAPS OF CARNIVOROUS PEATLAND PLANTS

Significant factors influencing the levels of individual micro- and macroelements in carnivorous plants include the age and the location of the trap. Some species have an ecophysiological adaptation which enables them to remove elements from ageing organs. The short (a few weeks) species-specific life cycle of the trap has an enormous impact on the development of the microbial community associated with it, which develops through periods of accumulation of organic matter, rapid decomposition, or mineral absorption (Sirová *et al.*, 2009).

The abundance of microorganisms increases in direct proportion to the age of the trap. Płachno *et al.* (2012) found that the microbiome in young traps was dominated by algae of the genera *Scenedesmus* spp. and *Characiopsis* sp., while in old traps *Scenedesmus* spp. and *Euglena* spp. were the most abundant taxa. The ciliate *Paramecium bursaria* was also more abundant in older traps (Płachno *et al.*, 2012). *Utricularia* traps acquire small amounts of food, but the number of microbes remains relatively high (Sirová *et al.*, 2009; Płachno *et al.*, 2012). The overall content of nutrients in the trap fluid is usually correlated with the age of the traps (Sirová *et al.*, 2009). The amount of C in the trap fluid relative to the tissue fluid increases in direct proportion to the age of the trap. Plant cells transport organic carbon to the traps, thus making it available to microorganisms (Sirová *et al.*, 2009).

EFFECTS OF OXYGEN CONDITIONS ON THE MICROBIOME

Traps become anoxic at night or during intensive digestion of organic matter (Sirová *et al.*, 2018). This is unfavourable for the microbiome, as the oxygen concentration in the trap is the main factor determining the life and multiplication of microbes. The internal structures of the traps and microorganisms consume oxygen relatively quickly. Despite some influx of oxygenated water to the traps and diffusion of O₂ from the cells of the trap wall, the internal structures of the traps are able to use it up quickly, causing anoxia (Adamec, 2007). The linear rate of decline, which is a measure of the respiration rate of the internal structures of the traps and commensal organisms, is compensated

for by the influx of oxygen through the trap walls (Giang *et al.*, 2015).

Studies by Vincent *et al.* (2011) and Adamek (2011) have shown that periods of hypoxia alternate with temporary periods of excess oxygen (Adamek, 2011; Vincent *et al.*, 2011). This mechanism may effectively kill the captured prey, but it may also impede the functioning of microorganisms. According to Płachno *et al.* (2012), the relatively low oxygen concentration in the traps of carnivorous plants limits microbial diversity and abundance (Płachno *et al.*, 2012). In contrast, Adamec (2011) reported that microorganisms present in the traps of carnivorous plants exhibit relatively high tolerance for variable environmental conditions, including frequent oxygen deficits (Adamec, 2011). According to Šimek *et al.* (2017), the physiological elasticity of various groups of microorganisms, involving a change from autotrophy to heterotrophy or vice versa, plays an important role, allowing them to adapt to dynamic environmental conditions. For example, ciliates can adapt to anoxic conditions owing to the strategy of mixotrophy (Šimek *et al.*, 2017). An experiment carried out by Studnicka (2003) showed that microbes with varied oxygen requirements can be present in the traps of plants of the genus *Genlisea* (Studnicka, 2003). This does not rule out the presence of facultative and obligate bacteria. Therefore commensal bacteria may be able to adapt to varied oxygen conditions (Giang *et al.*, 2015). Large amounts of peroxide and other reactive oxygen species are probably generated in *Genlisea* traps in order to kill prey, and they stimulate various oxidative stress reactions in the cells of traps (Giang *et al.*, 2015).

RELATIONSHIP BETWEEN WATER AND THE MICROBIOME OF CARNIVOROUS PLANTS

Previous research comparing the abundance of various groups of microorganisms and small Metazoa in water and in *Utricularia* traps has been published in only one paper (Mieczan and Bartkowska, 2022). The authors showed that elevated temperature significantly modifies the qualitative and quantitative structure of microbial communities. From 12 to 19 ciliate taxa were present in the water, but only 4 taxa were found in the microbiome of carnivorous plants (Mieczan and Bartkowska, 2022). Similar results were reported by Płachno *et al.* (2012), who showed low microbial diversity in carnivorous plant traps. The aquatic environment also exerts a strong effect on microorganisms through variable physical and chemical properties (Giang *et al.*, 2015).

The presence of water also has a significant dimension for evolution in the development of carnivorous plants. An experiment conducted by Freedman *et al.* (2021) showed that in an area with heavy rainfall, carnivorous plants formed larger traps which could hold more water and also influence the structure of the food web.

Despite differences in microbial communities depending on the environment, experimental research has shown that the microbiome of *Utricularia* traps may reflect the surrounding environmental conditions (Mieczan and Bartkowska, 2022).

FUNCTIONING OF THE FOOD WEB

The microbiome of carnivorous plants forms a complex network of trophic interactions (Freedman *et al.*, 2021). Giang *et al.* (2015) showed a significant relationship between bacteria of the *S. purpurea* microbiome and particulate organic matter (Fig. 6a). Mieczan and Bartkowska (2022) showed significant relationships between the total number of bacteria and the abundance of ciliates in *Utricularia* traps. The degree of correlation also differed between the main groups of microorganisms making up the food web, depending on temperature changes. At a temperature increased by 2°C, the total number of bacteria was positively correlated with the abundance of ciliates and flagellates. Raising the temperature by 4°C caused a positive correlation between the

abundance of heterotrophic flagellates and bacteria and the abundance of testate amoebae (Fig. 6b). Sirová *et al.* (2018) reported that plants of the genus *Utricularia* support the development of diverse microbial communities (within traps and on their surface). This enables digestion and utilisation of complex organic matter by populations of microorganisms, e.g. bacteria. This group of microorganisms has adapted to function in an environment with low oxygen supply, and also to protozoan predation (Adamec and Kondo, 2002). The presence of predatory Protozoa contributes to nutrient regeneration from the biomass of other groups of microbes, including bacteria and algae – Figure 6c (Sirová *et al.*, 2018).

The presence of eukaryotic organisms in the food web may differ depending on the habitat, as well as on the abundance of predators (Sirová, Adamec and Vrba, 2003; Gray *et al.*, 2012; Paisie, Miller and Mason, 2014; Grotjahn and Young, 2019). *Sarracenia*, a plant found over a vast area of eastern North America, has highly diverse microorganisms (Grotjahn and Young, 2019). In a study by Ellison *et al.* (2021), individual groups of bacteria were usually represented equally irrespective of the species of *Sarracenia* (Paisie, Miller and Mason, 2014; Ellison *et al.*, 2021). No single species was dominant in this genus, and the minor differences in the composition of microorganisms may have been due to mechanisms of bottom-up and top-down control within the food web (Bittleston *et al.*, 2018).

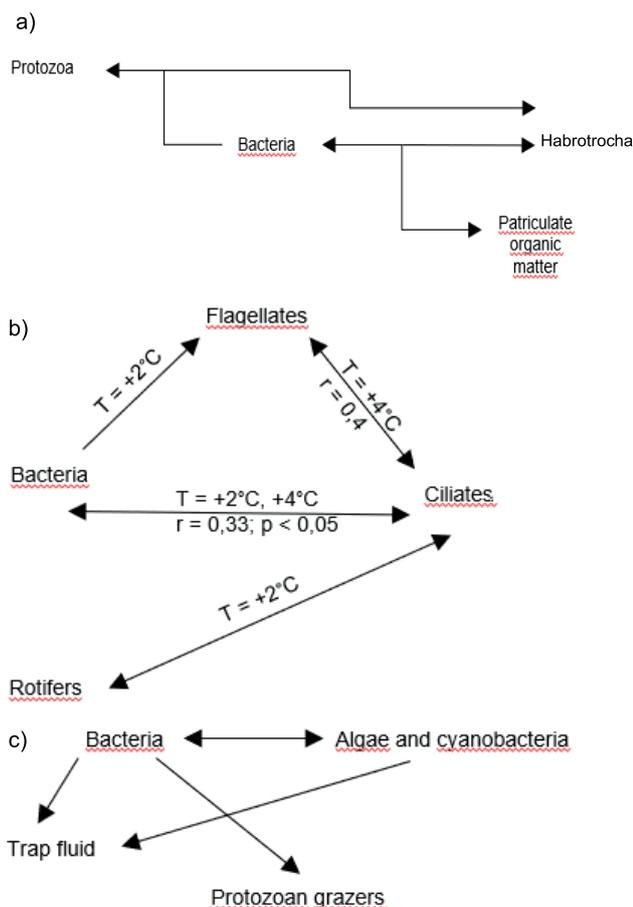


Fig. 6. Functioning of the food web: a) food web of *Sarracenia purpurea*, b) correlation between food web components in experimental microcosms of *Utricularia*, c) conceptual diagram of *Utricularia* trap ecophysiology; source: own elaboration based on: Giang *et al.* (2015), Sirová *et al.* (2018), and Mieczan and Bartkowska (2022)

CONCLUSIONS

1. The impact of increasing temperatures on the microbiome of carnivorous plants is poorly understood. A rise in temperature increases nutrient concentrations in the environment, resulting in increased abundance and biomass of microorganisms.
2. The short and species-specific life cycle of the trap has a major impact on the development of the microbial community associated with it, which develops through periods of accumulation of organic matter, rapid decomposition, or mineral absorption. The abundance of microorganisms increases in direct proportion to the age of the trap. Previous research has provided a fairly extensive explanation of the relationship between the age of the trap and the abundance of the microbes colonising it. It has been concluded that it may be dependent on the environment, and thus the microbiome of traps will reflect environmental conditions.
3. Future research must focus on the effect of ecological climate change on the microbiome of carnivorous plants, determine the relationships between temperature and trap size, and also determine the effect temperature and eutrophication on trophic interactions, not only between microorganisms, but also between organisms from higher trophic levels (e.g. rotifers, crustaceans, or larger invertebrates).

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