



General discussion

The first three chapters of this thesis aimed to explore the mechanisms behind tree diversity effects on carbon cycling in forests. Notably, we focused on microbial-based processes (Chapters I-III) and the consequences of tree diversity-induced spatial heterogeneity (Chapters I & III, Fig. 4). My colleagues and I considered several carbon cycling-related processes, such as tree biomass production, litterfall (Chapters I & III), litter decomposition (Chapter I), and *soil heterotrophic respiration¹* (Chapter II). In addition, we explored the relationships between the microbial community composition and functions, and how tree diversity influenced these relationships (Chapter II). Following, we synthesized these results with a whole-ecosystem approach of tree diversity effects on carbon cycling by considering tree diversity effects on the main carbon compartments and their relationships in forests (Chapter III). Finally, in the last chapter, we explored the implications of diversifying plantations and re-/afforestation projects to enhance carbon sequestration, and the mitigating climate change effects on forests and human well-being (Chapter IV). In this final section, I first summarized the main findings of my thesis and highlighted the implications for future research and our societies.

Main findings

In this thesis, my colleagues and I highlighted how tree diversity affects carbon cycling in forests (Chapter I - III, Fig. 7). We showed that tree diversity effects on carbon cycling are manifold by affecting all compartments (e.g., above- and belowground) and processes (e.g., litterfall, decomposition, soil respiration) of the carbon cycle in forests (Chapters I – III, Fig. 7). Finally, we discussed the implication of diversifying forests in plantations and during reforestation initiatives. Moreover, we explored the benefits of diversifying forests to mitigate

¹ words in *italic* are defined in the Glossary page 2

extreme climatic events and microclimatic condition effects on forests and human well-being (Chapter IV).

(i) My colleagues and I demonstrated the positive effects of tree diversity on tree productivity, including litterfall (Chapters I & III). By increasing the amount and diversity of litterfall, tree diversity increased litter decomposition, and thus, the assimilation of tree products into the forest soil (Chapter I).

(ii) Our investigation showed the key role of microbial communities in controlling carbon dynamics by carrying out litter decomposition (Chapter I), *soil heterotrophic* respiration (Chapter II), and soil carbon stabilization (Chapter III). In addition, we showed how tree diversity increased soil microbial biomass (Chapter I-III) and functions (Chapter I-II). Moreover, we highlighted that tree diversity effects on soil microbial respiration are mediated primarily by soil microbial biomass rather than soil microbial community taxonomic or functional diversity.

(iii) The effects of tree diversity on microbial biomass were mediated by biotic and abiotic environmental conditions such as root functional traits, tree productivity, soil chemistry, and microclimate (Chapters II & III). For instance, tree diversity increased microbial biomass by reducing the local temperature, and thus, indirectly increased microbial processes.

(iv) We demonstrated the importance of considering neighborhood scale to understand tree diversity effects on ecosystem functioning (Chapters I & III). For example, in Chapter I, we showed that increasing tree diversity increased the spatial heterogeneity of litterfall with consequences for litter decomposition. In addition, we revealed in Chapter III the importance of investigating the different spatial scales at which tree functional traits affect soil microbial biomass and soil carbon concentrations.



Fig. 7: microbial and spatial mediation of tree diversity effects on soil carbon cycling: visual summary of the main findings. Back arrows represent carbon fluxes between the different carbon compartments and processes (see Fig. 2). Red arrows indicate the results of tested relationships, a plus sign was added when the relationship was positive. Causal relations were drawn with single-headed arrows and correlations with double-headed arrows.

(v) We highlighted how planting diverse forests will promote climate change mitigation by increasing carbon fixation and storage, increasing forests resistance and resilience to climate change-induced threats (e.g., droughts, insect outbreaks), and mitigate microclimatic conditions in urban areas.

Together, our results suggest the crucial role of tree diversity in controlling forest functioning, the mechanisms behind tree diversity ~ carbon cycling relationships in forests, and the implication of diversifying forests for climate change mitigation.

Tree diversity effects on ecosystem functioning are manifold

Our results demonstrate the multiple effects of tree diversity on carbon cycling in forests by affecting every aspects (Fig. 7): from primary carbon inputs by photosynthesis (e.g., tree productivity, Chapters I & III) to the increase and stabilization of soil carbon by microbial transformation of freshly incorporated plant organic matter to stable microbial necromass (Chapter III, Buckeridge *et al.* 2020; Kästner and Miltner 2018). Moreover, we highlighted the interrelationships between all compartments and processes (Chapters I-III). For example, tree diversity increased on litter decomposition (Chapter I) by increasing the amount and diversity of litterfall and the microbial functioning (Chapter II). Due to these complex interrelationships, this thesis reinforces the need for whole-ecosystem approaches to better understand the effects of biodiversity on ecosystems (Kay *et al.* 1999; Potvin *et al.* 2011; Shepherd 2004).

These new insights from a manipulative tree diversity experiment highlight the key role of tree diversity in maintaining upper trophic level diversity (Chapter II, Singavarapu *et al.* 2021) and functioning (Chapter I-III). In addition, diversity and functioning of upper trophic levels (e.g., soil microbial community) are expected to promote tree diversity (Albert *et al.* 2021; see Plant-Soil Feedback theory, Crawford *et al.* 2019; Miki *et al.* 2010; Mangan *et al.* 2010; Putten *et al.* 2016). Therefore, my thesis suggests that tree diversity, by promoting favorable environmental conditions, would enhance upper trophic level diversity and functioning, and thus tree diversity (Fig. 8). This positive feedback loop of tree diversity on tree diversity would suggest the self-maintenance of diversity in natural systems. Therefore, to understand the long-term consequences of planting diverse forests, future research should explore the successions of plant communities following a species-rich plantation to understand the long-term ecosystem effects of planting species-rich communities.

Being bigger makes you stronger, but diversity helps too

Tree diversity effects on ecosystem properties and functions are various; however, we can highlight two mechanisms: mass (i.e., the consequences of tree diversity ~ productivity relationships, Sonkoly et al. 2019) and diversity effects (i.e., the consequences of increasing tree products diversity, Fig. 8). We showed that higher tree biomass affected several aspects of carbon cycling in forests, such as litterfall, decomposition, and soil carbon concentrations (Chapters I & III). Moreover, we found similar mechanisms at the microbial community level, where increasing microbial biomass increased microbial respiration (Chapter II). In addition, we provided some evidence of diversity effects. For example, higher litter diversity increased litter decomposition (Chapter II), while crown structural complementarity reduced air temperature (Chapter III). Taken together, these results highlight the causal relationships behind tree diversity effects on forest functioning, as well as the complexity of the causal cascade resulting from these multiple causal relationships. For example, our results suggest a positive effect of tree diversity on soil microbial biomass due to changes in environmental conditions (Chapter III), while increasing soil microbial biomass promotes heterotrophic respiration (Chapter II) and soil carbon stabilization (Chapter III, Buckeridge et al. 2020; Kästner and Miltner 2018).



Fig. 8: Diversity (in red) and mass (in green) effects of tree diversity on ecosystem functioning (adapted from Fig. 3).

Tree diversity-induces spatial heterogeneity

A significant contribution of this thesis is the first demonstration that forest spatial heterogeneity is driven by tree diversity (Chapters I & III). Together with previous results showing higher crown (Perles-Garcia et al. 2021; Williams et al. 2017) or root (Guillemot et al. 2020) complementarity with increasing tree diversity, our results suggest that tree diversity effects on forest spatial heterogeneity are crucial to understand tree diversity effects on upper trophic level communities and functions. Moreover, the sessile nature of trees and the distancebased distribution of tree products (e.g., litter, Chapter I, Chandler et al. 2008) have structural consequences for the whole ecosystem, as shown in Chapters I & III; therefore, increasing tree diversity will per se will increase the forest heterogeneity. Our results suggest that the effect of tree-induced spatial heterogeneity appears at the local scale; however, how the spatial organization of tree species affects ecosystem functions remains unclear at the plot-level. For instance, parameters such as planting distances and spatial organization of tree species may become critical for forest functioning (Antony et al. 2012; Brazier and Mobbs 1993; Otsamo 2002; Uselis *et al.* 2020). Moreover, the distance-based effect of tree species may promote the non-linear distribution of products and lead to non-linear effects of tree diversity at the plotlevel. Thus, estimates of processes such as decomposition or carbon storage at the plot level may differ greatly from traditionally measured averages. Therefore, this work emphasizes the need to consider the spatial distribution of forest processes and their relation to tree diversity in our sampling methods. Moreover, tree spatial distribution will determine possible tree-tree interactions. Tree-tree interactions may be crucial for ecosystem functioning (Fichtner et al. 2018). For instance, Fichtner et al. (2018) emphasized the importance of tree-tree interactions at the neighborhood scale to understand tree diversity effects on productivity. Therefore, treetree interactions are determined by tree diversity and the spatial distribution of tree species in the plot, highlighting the importance of local spatial scales for ecosystem functioning (Fichtner *et al.* 2018; Williams *et al.* 2017) and suggesting a high spatial heterogeneity of interactions within forests.

Subtropical forest carbon cycle under microbial-control

Microbial communities are crucial for maintaining key ecological processes such as nitrogen fixation and nitrification. My results demonstrated role of microorganisms in controlling carbon cycling processes in subtropical forests (e.g., litter decomposition, Chapter I). Therefore, we showed that forest processes are driven by microbe, and we provided some first keys to understand tree diversity effects on soil microbial communities (Chapter II-III). However, our understanding of microbial community dynamics in forests remains scarce (Yokobe et al. 2018). For instance, litter is the primary interface between aboveground (Fanin et al. 2021) and belowground microbial communities. Before litterfall, leaves are exposed to the aboveground microbial community (Saadani et al. 2021); during litterfall, leaves get in contact with the belowground microbial community (Singavarapu et al. 2021). Therefore, litter decomposition is conducted by a mixed community resulting from the assemblage between aboveground and belowground microbial communities. However, little is known about the processes that lead to the formation of the decomposer community. We need to measure and follow the leaves' microbial community dynamics to better grasp microbial decomposition and the relative contribution of above- and belowground microbial communities. Here, both experimental and simulation-based approaches are needed to understand leaf microbial community dynamics and their drivers (Fanin et al. 2021).

Tree diversity control over environmental conditions

In Chapter III, we bring some first pieces of evidence for the control of tree diversity on microclimate promposed by Gottschall *et al.* (2019). In addition, in Chapter IV, we highlighted the potential of tree diversity to mitigate *extreme climatic events* (e.g., drought, flood) effects on tree productivity (Fichtner *et al.* 2020; but see Grossiord 2020 for context-dependencies),

and subsequently the implications for forest functioning (Schnabel *et al.* 2019). By stabilizing microclimatic conditions and reducing *extreme climatic events* effects on ecosystem function, tree diversity stabilizes ecosystem functions (Schnabel *et al.* 2019) and thus ecosystem services provided to human populations (FAO and UNEP 2020; Fichtner *et al.* 2020). However, the mechanisms linking tree diversity to microclimatic conditions remain unknown and require further investigation to understand the consequences of microclimatic buffering for ecosystem functioning.

Planting diverse forests to mitigate climate change

As suggested in Chapter IV, the positive effects of tree diversity on carbon storage in forests would help to maximize the potential of re-/afforestation initiatives to mitigate increasing atmospheric carbon and thus climate change (Bastin *et al.* 2019; Lewis *et al.* 2019). However, where and how diversifying forests is feasible remains to be identified (Holl and Brancalion 2020). For example, reforestation projects may lead to critical pitfalls such as reducing water availability and increasing soil salinity (Jackson *et al.* 2005) or exacerbating population inequalities (Holl and Brancalion 2020). Therefore, we need to clarify where re-/afforestation projects would be beneficial and how tree diversity could maximize these projects. In other words: we need to figure out "where" trees should be planted and "which" tree community should be planted. Therefore, the increasing availability of inventory data (Craven *et al.* 2020) together with the global network of tree diversity experiments (TreeDivNet, Verheyen *et al.* 2016) are promising initiatives to quantify tree diversity potential to mitigate climate change. In addition, few reforestation projects report progress and success rates, limiting our ability to learn from past experiences (Martin *et al.* 2021). Therefore, initiatives like Restor² will provide

² <u>https://restor.eco/</u>

unparalleled feedback for future projects and prevent us from repeating our mistakes (Holl and Brancalion 2020; Jackson *et al.* 2005).

Perspectives for future research

This thesis provides initial insights into tree diversity-induced spatial heterogeneity (Chapter I & III). Further research should focus on this second layer of diversity: the spatial heterogeneity of tree products, itsfunctional drivers, and the consequences for the overall food web and its functions (Fig. 3). According to my results, this new intermediate level representing the spatial heterogeneity within the ecosystem may become crucial to understand tree functions (e.g., productivity) and higher trophic levels drivers and functions (Chapter III). Le Provost *et al.* (2021) presented a spatially explicit framework by looking at aboveground and belowground diversity drivers across spatial scales: landscape-level (500-2000 m radius around the sampling point), field-level (75 m radius), and plot-level (50 – 50 m). Therefore, I would suggest extending this framework to a finer scale (i.e., within the ecosystem functions. Following Le Provost *et al.* (2021), I would expect tree diversity-induced spatial heterogeneity to explain part of the plot-level heterogeneity, and thus the higher trophic level abundance, diversity, and functions.

Our understanding of tree diversity effects on ecosystem functioning may gain from exploring tree diversity-induced spatial heterogeneity; moreover, the effects of tree diversity on forest temporal asynchrony remain poorley understood (Fig. 3). This is especially true for the relationship between tree phenology and consumers phenology (van Schaik *et al.* 1993; Seifert *et al.* 2021). In their publication, Seifert *et al.* (2021) showed that herbivore community specialization increases between spring and fall, suggesting synchrony between leaf dynamics and herbivore community dynamics. Therefore, in species-rich forests that exhibit diverse tree phenology (Du *et al.* 2019; Huang *et al.* 2017), we might expect tree diversity-induced temporal asynchrony to drive consumer community and thus ecosystem functions. Further investigations

are needed to tackle this facet of tree diversity by following tree and consumer phenology across seasons and the consequences for ecosystem functions. Specifically, increasing tree litterfall asynchrony between the species will increase the number of freshly fallen litter inputs. Fresh litter inputs are expected to enhance litter and soil decomposition by a priming effect on the microbial community (Xu *et al.* 2018). Therefore, we would expect tree diversity to increase litter and soil decomposition by enhancing the fresh litter priming effect after each species fall.

Investigating spatio-temporal scales at the plot level requires high resolution and high temporal repetition of measurements (Gottschall et al. 2019). However, our current sampling methods are both limited in terms of resolution and unsustainable, often prioritizing efficiency over sustainability (Meyer et al. 2015). For instance, our first soil sampling in September 2018 required about 200 g of soil per sample to measure soil microbial community composition, biomass, physiology (MicroResp®), and respiration. Such a demand is not sustainable for repeated small-scale samplings. Moreover, mapping tree roots is often destructive as the entire root system must be excavated. Non-invasive methods for sustainable sampling are essential for investigating temporal and small spatial scales. One might look at the forest (above- and/or belowground) from three lenses: its physical structure (spatial arrangement and abundance of the different structural components such as branches, roots, rocks ...), its chemical structure (i.e., the chemical composition such as soil carbon and nitrogen content, humidity), its biological structure (i.e., food web structure and biological processes such as decomposition), and external abiotic parameters such as temperature. Abovegroung, non-invasive methods to measure these different facets of the forests are numerous (Fig. 9); for instance, Terrestrial Laser Scanning used by Perles-Garcia et al. (2021) to measure aboveground physical structure, camera traps can be used to identify aboveground arthropod community (Droissart et al. 2021; Moore et al. 2021), caterpillar dummies to measure predation rate (Low et al. 2014; Howe et

al. 2009), and projects like AMMOD³ allow for automated counting and identification of aboveground arthropod and plant species at larger scales. In addition, indirect methods such as measurements of the soundscape (Pijanowski et al. 2011) and smellscape (e.g., volatiles compound measurements; Tholl et al. 2021; Xiao 2020) are gaining importance and efficiency for determining species presense and dynamics. However, much progress is still needed belowground to widely open the "black box" (Fig. 9). For instance, new technologies based on X-ray (Mooney et al. 2012) and acoustic tomography (Bearce et al. 2014; Blum et al. 2004) are promising to improve mapping of soil structure (e.g., root, inorganic matrix, water, and air). However, these methods are still in the early stage of development and are not yet designed for in situ measurements. Likewise, a new method of mid-infrared spectrometry measurements would provide portable and non-invasive methods of soil chemistry (Ji et al. 2016), while requiring only a small amount of soil. Simultaneously, new sensors like EDAPHOLOG are promising avenues to identify and track soil microarthropods in situ (Dombos et al. 2017). However, measuring and identifying microbial communities and processes remains complex and soil consuming; some new methods are moving toward sustainability, for instance, in situ monitoring of microbial activity (Jin et al. 2020). In this vein, a method that consist in inserting and measuring chips will prevent repeated disturbances to the soil matrix and its communities. For example, methods like bait-lamina strips (Hamel *et al.* 2007) and TeaBags⁴ (Keuskamp *et* al. 2013) to assess soil activity and decomposition, or microfluidic chips to sample soil microbial communities (Mafla-Endara et al. 2021; Pucetaite et al. 2021) are likely to gain importance in the coming years. Altogether, promising avenues consist in non-invasive measurements using tomography mapping of soil structures (e.g., seismic, acoustic, X-ray), spectrometry measurements of soil chemistry, image-based detection of soil organisms (e.g.,

³ https://www.fona.de/en/measures/funding-measures/ammod_copy.php

⁴ <u>http://www.teatime4science.org/</u>

EDAPHOLOG), and removable sampling chips (bait-lamina strips or microfluidic chips). All these previously mentioned methods should now be promoted in soil sciences to support the high spatial and temporal resolution of our samplings.

My thesis highlighted that tree diversity effects on ecosystem functioning are multifactorial and follow many pathways; therefore, having a holistic view of the ecosystem requires that numerous disciplines work together. Through this thesis, my colleagues and I promoted interdisciplinary approaches by bringing together experts of different fields such as plant ecologists, soil ecologists, cartographers, and microbiologists. The development of such interdisciplinary team is now a prerequisite for synthesizing broader research questions beyond disciplines like biodiversity-ecosystem functioning relationships (Kelly et al. 2019). Therefore,

		Physical structure: - Terrestrial Laser Scanning ¹ - Tree inventory data ² - Thermal imagery ³ - Remote sensing ⁴	Fig. 9: Above- and belowground non-invasive measurement methods to access abiotic conditions and physical, chemical and biological structure of forests.
*	, ≥, PC	Chemical structure: - Air quality sensors ⁵ - Leaf spectrophotometry ⁶ - Smellscape ⁷	Methods in italics are in development and not yet operational <i>in situ</i> . <u>References:</u> ¹ : e.g. Kunz <i>et al.</i> (2019), Perles-Garcia <i>et al.</i>
₩6		Biological structure: - Camera traping ⁸ - Dummy caterpillars ⁹ - Cafeteria experiments ¹⁰ - Soundscape ¹¹	 (2021) ²: Avery and Burkhart (2015) ³: Still <i>et al.</i> (2019); ⁴: Wang and Gamon (2019) ⁵: Piedrahita <i>et al.</i> (2014) ⁶: Perez-Harguindeguy <i>et al.</i> (2013), e.g.
	J	Abiotic condition: - Pluviometer, anemometer ¹²	Davrinche and Haider (2021) ⁷ : e.g. volatile organic compounds Tholl <i>et al.</i>
		 humidity, temperature sensors¹³ Soil physical structure: Tomography (X-ray, acoustic)¹⁴ Minirhizotron¹⁵ 	 (2021) & Xiao (2020) ⁸: Dell <i>et al.</i> (2014) ⁹: Low <i>et al.</i> (2014), Howe <i>et al.</i> (2009) ¹⁰: Grime <i>et al.</i> (1996) ¹¹: Pijanowski <i>et al.</i> (2011) ^{12,13}: e.g. RX2100 Data Logger, HOBO Pendant® (ONSET, Bourne, USA) ¹⁴. Bearce <i>et al.</i> (2014) Blum <i>et al.</i> (2004)
	N PC	Soil chemical structure: - Soil spectrometry (in situ) ¹⁶ - pH and chemical sensors ¹⁷	¹⁵ : Svane <i>et al.</i> (2012) ¹⁵ : Svane <i>et al.</i> (2019) ¹⁶ : Ji <i>et al.</i> (2016) ¹⁷ : e.g. HOBOnet T21 (ONSET, Bourne,
	36) 36)	 Soil biological structure: EDAPHOLOG¹⁸ Microfluidic chips¹⁹ Bait-lamina strips²⁰ Enzyme measurement in situ²¹ Decomposition experiments²² 	USA) ¹⁸ : Dombos <i>et al.</i> (2017) ¹⁹ : Mafla-Endara <i>et al.</i> (2021) ²⁰ : Kratz (1998), Eisenhauer <i>et al.</i> (2014) ²¹ : Wallenstein and Weintraub (2008) ²² : Keuskamp <i>et al.</i> (2013)

cohorts of doctoral researchers such as TreeDì in BEF-China (Trogisch *et al.* 2020) and in the Jena Experiment⁵, provide nice examples of *interdisciplinary* teams built around a broader research question. However, one may question the feasibility of such *interdisciplinary* research in the context of a Ph.D. considering the duration of a doctoral project (e.g., three to four years in Germany) and of research fundings. This is especially true for time-related measurements which require years to build time series replicates. Therefore, to advance the understanding of temporal dynamics, long-term monitoring is needed to serve as a basis for these experiments.

Perspectives for our societies

This study is a step forward to the understanding of forest ecosystem functioning. Understanding the mechanisms shaping forests and driving their functions is critical to be able to predict biodiversity loss consequences on the potential ecosystem services such as wood production (FAO and UNEP 2020) or climate mitigation (Bastin *et al.* 2019; Lewis *et al.* 2019; IPCC 2013). Our results suggest that increasing tree diversity should enhance wood production as well as carbon storage (Chapter III, Xu *et al.* 2020). Moreover, tree diversity effects on these ecosystem services could be enhanced by selecting tree species base on their functional traits such as root and leaf characteristics. Together, these results are the first step to the prediction of ecosystem functioning and thus to our ability to provide accurate and efficient recommendations to practitioners. However, our results should be integrated into a larger framework to not only optimize few ecosystem functions, but also consider practitioners' needs and constraints (Messier *et al.* 2021). For instance, when tree productivity is a sufficient response variable for firewood production, millwork processes will require high-quality lumber (see ISO standards; Messier *et al.* 2021). In addition, our results suggest the relevance of tree-tree interactions and thus the importance of considering tree-tree interaction to guide planting

⁵ <u>http://the-jena-experiment.de/index.php/projects/</u>

patterns in plantations and reforestation projects. Therefore, "planting diverse forests" may be an oversimplification of a problem that requires a higher integration of spatial, economic and social constraints (Messier *et al.* 2021). For example, if the goal of a planted forest is both storing carbon and producing wood for millwork, both aspects should be integrated into our research of suitable tree communities. Such questions can be solved by integrating goals (e.g., carbon storage and wood production) and their drivers (e.g., tree diversity, tree functional traits, including wood quality) in a simulation framework to predict ecosystem direction (Gaucherel *et al.* 2017; Gaucherel and Pommereau 2019). This approach would help us provide accurate and personalized recommendations to the practitioners (Mao *et al.* 2021; Messier *et al.* 2021). Exploring applicable and operational guidance for practitioners requires a greater *transdisciplinary* in BEF research to meet BEF goals and the practitioners' needs and constraints (see Chapter IV; Mao *et al.* 2021).

Finally, in times of international pandemic, global climate change, and loss of biodiversity, the relation between the scientists and the public becomes increasingly important to provide reliable information to the public. In particular, *science communication* makes it possible to demystify science for the general public by explaining both methods and results. Therefore, *science communication* is critical to provide reliable information to the public and fight conspiracy theories and fake news (Lewandowsky *et al.* 2017; McGee and Dawson 2020). In my opinion, engaging in *science communication* projects is not an option but a requirement for scientists, as is peer-reviewing (Tennant 2018). Consequently, more and more *science communication* projects are growing up, especially to inform and exchange with younger generations. The journal Frontiers for Young Minds allows researchers to write down their research for kids and young adults and provide a peer-reviewing by a scientific mentor and a young reviewer⁶. As part of this effort, Helen Philipps, Malte Jochum, and I edited a collection

⁶ <u>https://kids.frontiersin.org</u>

about Soil Biodiversity⁷ in Frontiers for Young Minds in the past few years to provide

information about soil biodiversity, its drivers, and its functions.

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⁷ https://kids.frontiersin.org/collections/11796/soil-biodiversity

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