

Post-fire succession in the northern pine forest in Russia: a case study

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Summary: This work describes the post-fire succession pattern of the pine forest on the Oleniy Island, White Sea, during the first twelve years of its recovery. We analyzed two separate cases of post-fire succession which differ in the degree of initial soil damage. Investigated factors included total projective cover (TPC) and abundance of individual plant species. Multivariate data analysis revealed that the rate of recovery was relatively stable at the better preserved site and changed from almost zero to higher values at the more damaged site. The difference in species composition at the two sites increased over time, indicating diverging succession patterns. While the genus *Vaccinium* mostly contributed to similarities in the site development, *Ledum palustre* and *Equisetum sylvaticum* (from the better preserved site) and *Pinus sylvestris* and *Calluna vulgaris* (from the less preserved site) were responsible for the disparities in the succession flow.

Keywords: post-fire succession, fire, northern pine forest, recovery, soil damage, total projective cover, individual species, species composition, rate of recovery, dominant species

Fire is regarded as one of the most important environmental factors determining the vegetation of the Earth. As a result of human activity, its impact has significantly increased (VAKUROV 1975; HYTTBORN et al. 2005). Usually the forest fire has a short but powerful damaging effect on plants; as a result, most vegetation and the forest litter are burnt. In some cases, a particularly strong surface fire also partially destroys the soil (BOND & WILGEN 1996; GROMTSEV 2000).

Post-fire succession is a typical example of secondary succession. Its main feature is a gradual change in ecosystems, initially accompanied by an increase in the number of species as well as in the total biomass of organisms. Changes in plant biomass can be indirectly tracked via the projective cover, i. e. the relative area of their projections on the surface of the soil (ZYRYANOVA et al. 2010). The speed of these processes decreases after several years: after a certain point, succession stages tend to differ from climax by their composition and stability, not by abundance and variety of flora (GROMTSEV 2000). Species number and projective cover are reported to grow sufficiently only during the first three years after the fire. (KUULUVAINEN & ROUVINEN 2000; WANG & KEMBALL 2005).

Another feature of succession is a change in life strategies of inhabiting species. Ruderal species prevail in the early years; soon they become accompanied by tolerant species, resilient to the harsh conditions of a post-fire ecosystem. Eventually such plants are replaced by more competitive successors which reproduce less quickly, but can supplant other species. A higher level of forest damage corresponds to a lower rate of transition between the species (RUOKOLAINEN & SALO 2009).

Some plants benefit from improved light conditions, availability of mineral elements and a sharp decline in competition and therefore are well adapted to post-fire conditions (e.g. CALVO et al. 2008). This fact is well-known in many human cultures; nineteenth-century peasants in Siberia

even set forests on fire in order to increase the growth of cowberry (*Vaccinium vitis-idaea*), which could grow quickly from its unharmed subterranean buds (GROMTSEV 2002). Pine (*Pinus* spp.), one of the most widespread genus in northern forests, not only survives after natural fires, but also adopts new territories due to the removal of its less adapted competitors (RAZUMOVSKIY 1999; HYTTEBORN et al. 2005).

Currently, there are no scientific works presenting a quantitative analysis of post-fire succession patterns in Northern Europe pine forest. Available publications described succession only during first several years or, alternatively, decades after the fire (e.g. KUULUVAINEN & RUOVINEN 2000; WANG & KEMBALL 2005; RUOKOLAINEN & SALO 2009). Moreover, the Northern pine forest close to the border of taiga zone has not been a subject for thorough, long-term research. Nowadays, the only relatively undisturbed forests in Europe are located in Russian Karelia (LAMPAINEN et al. 2004). In this work, we studied two pine forest sites in Russian Karelia with different levels of damage. In order to evaluate the influence of fire damage levels on succession flow, we formulated and checked several hypotheses:

- In forest areas with burnt soil the rate of succession in the early years will be significantly reduced in comparison to areas with preserved soil.
- The succession series on sites with preserved soil will change more gradually than those on sites with burnt soil.
- During the years of observation, the number of species will continue to increase on both sites.
- Replacement of dominant species in the course of succession will occur more often in areas with burned soil than in areas with preserved soil.
- The succession pattern and the sets of species will become more similar on the two sites over time.

Materials and methods

Data collection

The explored sites were part of a pine forest on island Oleniy. The island (2.7 km²) is located in the Chupa Inlet of the Kandalaksha Gulf, the White Sea, Russian Karelia and belongs to the Keretskiy refuge. At the end of July 2000 the northeast of island was on fire; at least 30% of the forest was burnt (A. Shipunov, pers. obs.).

In order to observe the progress of the post-fire succession on the Oleniy Island, two sites with a typical size of 10 × 10 m (GROMTSEV 2000) were marked: site A (N 66° 18' 54.6"; E 33° 27' 09.0") and site B (N 66° 19' 00.6"; E 33° 27' 13.1"). In 2012 we established three new sites with a size of 8 × 8 m, namely site IA (located 15 m to the south-east from site A), site IB (located 30 m to the west from site B) and site IIB (located 60 m to the west-north-west from site B). Group A sites were situated in the less damaged part of the forest (in the edge of a bog), while group B sites were found in the area with burnt soil (in a dry heather pine forest). The new sites were established in order to check whether, (a) the initial sites differed in floristic composition, because they were affected by the fire to a different degree, or (b) the differences were caused by incidental causes.

Each year from 2001 to 2012 inclusive we estimated the projective cover of higher plants species at both sites in late July to early August. In addition, we marked the degree of dominance of

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higher plant species in the community on the seven-point scale (0 = the species is absent; 1 = one exemplar; 2 = under 10 exemplars; 3 = more than 10 exemplars, but no more than 5% from the total abundance of plants on the site; 4 = 5–25% from all plants; 5 = 25–50%; 6 = 50–75%; 7 = 75–100%). The size of the sites allowed us to observe the presence of all vascular plant species.

Statistical analysis

We analyzed our data using R statistical environment (R DEVELOPMENT CORE TEAM 2012). We compared the total projective cover on the two sites as well as the number of species using Wilcoxon rank sum test for non-parametric data. The sample size for each site was 12, same as the number of years of observation. Additionally, we calculated the Shannon diversity indices for flora composition at each site for each year.

To explore the general trends in succession, we performed the principal component analysis. The object of classification was the floral species composition of each site in a given year; the principal components described the effect of each plant species on site development. We also derived the loadings of each species on the first and second component.

Finally, to find out the species co-occurrence, we used cluster analysis that was based on species composition and distribution between the sites. The analysis included 21 species, which were separated according to their influence on succession on both sites.

Results

Individual species

During the time of observation, only a few species were common for both sites. However, these species (*Vaccinium myrtillus*, *V. vitis-idaea* and *Pohlia nutans*) were relatively abundant (their average projective cover was 12%, 6.3% and 1.7% respectively). Aspen (*Populus tremula*) also developed at both sites, although in considerably smaller numbers: a few seedlings were observed at site A each year except 2004. At site B, several aspen plants appeared every year starting from 2007. *Pinus sylvestris* thrived at site B, where it occupied 0.5–1% of the total projective cover in the last years of observation. It was also registered once (in 2004) at site A.

Several plant species, namely *Equisetum sylvestris*, *Ledum palustre*, *Luzula pilosa*, *Melampyrum pratense* and *Orthilia secunda*, were unique for site A. The site was also characterized by the presence of small shoots of *Betula pubescens*. The species specific for site B were *Calluna vulgaris*, *Salix caprea* and *Chamaenerion angustifolium*.

The moss layer developed rapidly at both sites. The most common species was *Pohlia nutans*, appearing in 2003 at site A and occupying as much as 10% in 2010; at B, however, it appeared in 2004 but never exceeded 2%. Another moss, *Polytrichum juniperinum*, appeared at sites A and B in 2004 and 2003 respectively, but its cover at site A never exceeded 1%, while at site B it occupied 30% by 2011. Some other moss species were present at site A (*Polytrichum commune* in 2002–2011, *Dicranum* spp. in 2007–2011 and *Pleurozium schreberi* in 2007 and 2011), but none of them occupied a significant area.

When compared with control sites, sites A and B displayed some differences in species composition that were characteristic of their groups. The only species present at all sites was *Vaccinium*

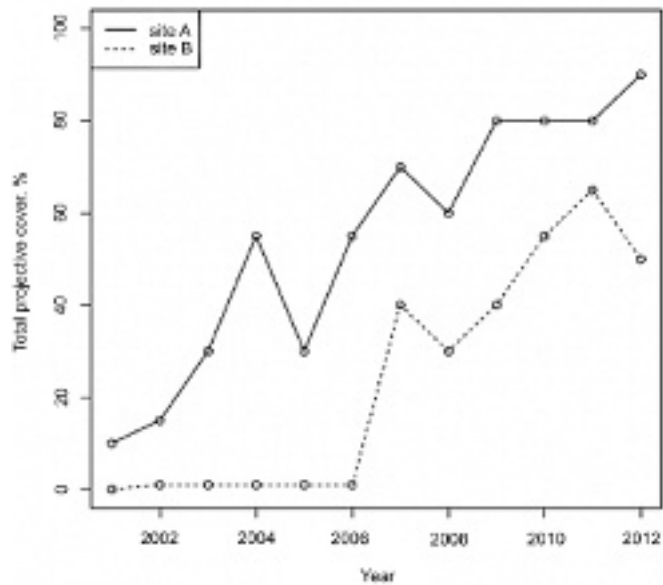


Figure 1. Total projective cover in 2001–2012 on the sample sites A and B. The precision of evaluation of the TPC values was 5%.

vitis-idaea, *Equisetum sylvestris*, *Ledum palustre*, *Melampyrum pratense* and *Betula pubescens* were common for both group A sites. Site IA also featured two species which were not observed on site A during all years: *Salix caprea* and *Vaccinium uliginosum*.

Sites IB and IIB contained species that were characteristic of the original site B, namely *Pinus sylvestris*, *Calluna vulgaris* and *Chamaenerion angustifolium*. *Populus tremula* developed at site IB, but not at site IIB. *Salix caprea* was absent at sites IB and IIB (as well as at site B in 2012). The common species among mosses, *Pohlia nutans*, was present at all sites except IA, while *Polytrichum*

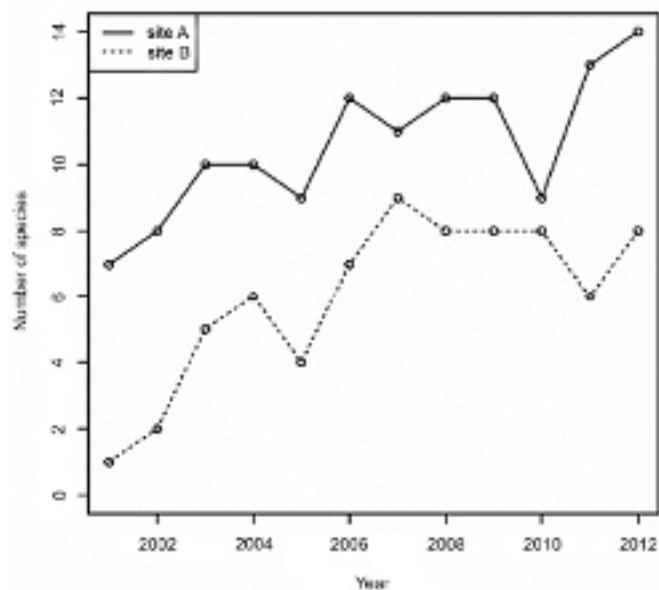


Figure 2. The number of species in 2001–2012 on the sample sites A and B.

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juniperinum appeared at all sites. Besides species typical of group A sites, *Polytrichum commune* and *Dicranum* spp., site IA contained *Pleurozium schreberi* and *Hylocomium splendens*, the latter of which had not been registered at other sites.

The total projective cover (TPC)

The TPC at site A was greater than that at site B for every given year (Fig. 1); the difference was statistically significant (Wilcoxon rank sum test $W = 98$, $p = 0.0025$). While TPC at site A was constantly increasing, TPC at site B was initially low, exceeding 1% only in 2007.

Species composition

In all years of observation the site with preserved soil contained more plant species than the site with burnt soil (Fig. 2). The difference was statistically significant (Wilcoxon rank sum test $W = 113$, $p = 0.0024$). Moreover, at B the number of species increased almost every year, while at site A it fluctuated starting from 2003 (Fig. 2). Shannon diversity indices for the two sites follow a similar pattern (Fig. 3).

Dominant species

Species that occupied more than 25% of the TPC were considered dominant. At site A, *Vaccinium myrtillus* prevailed most of the time; for the first two years its co-dominant was *Ledum palustre*. In 2005 *Vaccinium myrtillus* was temporarily replaced by *Vaccinium vitis-idaea*, but the next year its dominance was restored.

At site B, the abundance of the species was initially too low to determine the dominants. However, it was clear that in the first years the projective cover of *Vaccinium vitis-idaea* was greatest. Starting from 2009, there was a clear shift to the dominance of *Calluna vulgaris* which prevailed all the subsequent years.

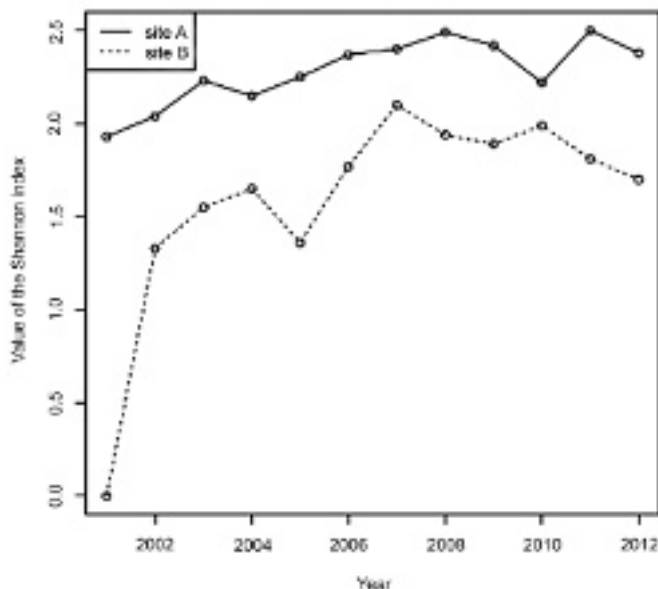


Figure 3. Shannon diversity index in 2001–2012 on the sample sites A and B.

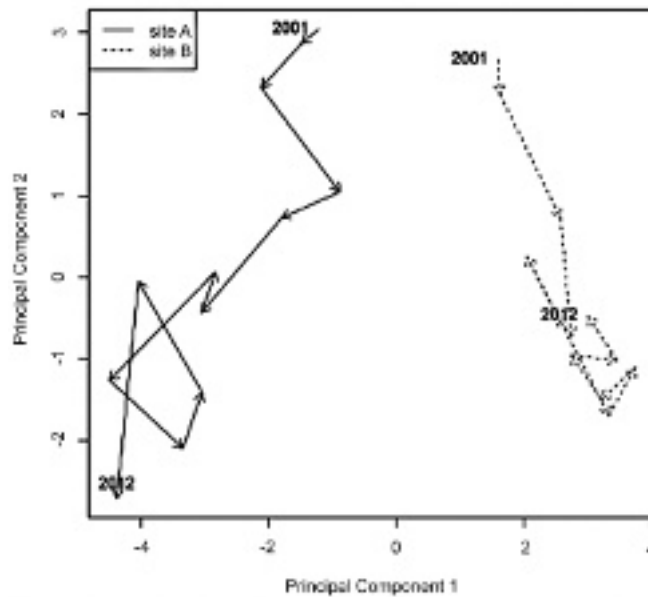


Figure 4. Principal component analysis of relative abundance of all the species on the sites A and B. The first year (2001) and the last year (2012) of the observation are marked.

Multivariate analyses

We evaluated changes in species composition at both sites using the principal component analysis based on relative abundances of species (Fig. 4). The principal components reflected the impact of species on the overall site development.

The succession patterns at the two sites diverged for the first component, but moved in the same direction for the second. Principal component loadings demonstrated that abundances of *Ledum palustre*, *Pohlia nutans* and *Equisetum sylvaticum* were most influential on the first component, whereas the second component was determined primarily by the abundances of *Vaccinium vitis-idaea*, *Dicranum* spp. and *Chamaenerion angustifolium*.

We used cluster analysis to investigate species co-occurrence (Fig. 5). One of the discovered stable groups was composed of *Vaccinium myrtillus*, *V. vitis-idaea* and *Pohlia nutans*; another group comprised *Ledum palustre* and *Equisetum sylvaticum* (both species were present only at site A, occupying relatively large areas). Finally, *Pinus sylvestris* and *Calluna vulgaris*, species that were widespread at site B, also constituted a stable cluster; in most cases they were accompanied by *Polytrichum juniperinum*.

Discussion

Individual species

At the less damaged site A, the first species to recover were those with horizontal shoots partially covered by soil, which made them less susceptible to fire (*Vaccinium myrtillus*, *V. vitis-idaea*, *Ledum palustre* and, possibly, *Equisetum sylvaticum*). Plants that appeared at the sites in the form of seeds or spores also recovered quickly (*Equisetum sylvaticum*, *Melampyrum pratense*). Their rapid regeneration can be associated with reduced competition after the fire. The fire did not damage the roots of trees *Betula pubescens* and *Populus tremula*, which allowed them to develop

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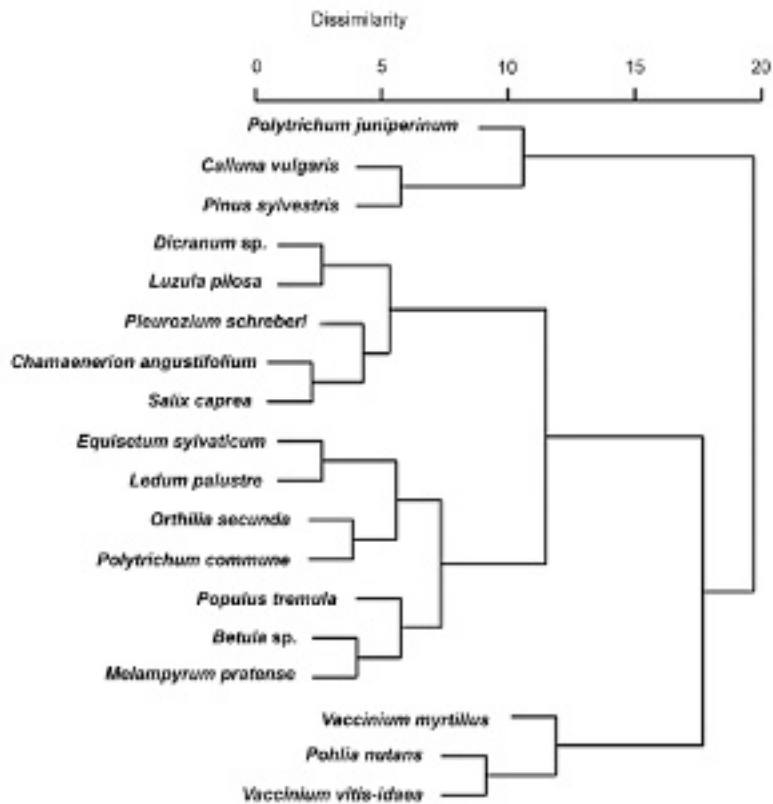


Figure 5. Cluster analysis for the species composition at sites A and B in 2001–2012.

shoots one year after the fire. Rapid development of shrubs at site A probably contributed to the poor development of its moss component: the most abundant moss *Pohlia nutans* never occupied more than 10% of the TPC, while at site B the cover of *Polytrichum juniperinum* reached as much as 30%.

In the more damaged site B not only the vegetation but the surface soil layer was destroyed. Therefore, among seed plants, only those with anemochorous distribution (like *Pinus sylvestris*) could develop. Developed moss cover did not prevent pine seedlings from growing, like it did at later succession stages (STEIJLEN et al. 1995; TIMO & SEPPÖ 2000).

The fireweed (*Chamaenerion angustifolium*), a typical plant of burnt forests, appeared only in small numbers in the seventh year after the fire. Its previous absence is probably caused by the fact that the distribution of its wind-dispersed seeds is hampered in the forest. Later, tree density decreased as burnt trunks fell down; thus, fireweed seeds could disperse more freely.

Those sites that were located in areas affected by the fire to a similar degree had similar species composition, i. e. site IA was similar to site A, while sites IB and IIB resembled site B. Proceeding from this data, we can say that the differences in species composition at sites A and B were specifically caused by the level of damage during the fire.

The total projective cover (TPC)

The constant increase of TPC at site A was most likely caused by the abundance of resources (light, water, and ash minerals), as well as by reduction in plant competitiveness. While resources

at site B were also sufficient, a strong fire created unfavorable conditions by partially destroying the soil. Consequently, seed recovery prevailed at site B, so most vascular plants appeared only several years after the start of observation.

Our hypotheses regarding the rate of succession were confirmed. Increase in TPC at the site with partially destroyed soil was lower than at the site where it was preserved. Overall, TPC can serve as an indicator of the succession progress, at least during the first decade after the disturbance. It reflects the rate of succession as well as the differences in the stages of recovery at the two sites. Constant growth of TPC contradicts the findings of WANG & KEMBALL (2005), who indicate that TPC would become stable three years after the fire.

Species composition

As expected, the number of species and the diversity index depended on time, i. e. on the succession stage. However, this correlation was less apparent at site A, probably because it was undergoing later stages of succession. As a result, in some years the number of species was constant or even decreased in agreement with the data of KUULUVAINEN & RUOVINEN (2000). Contrary, at site B the number of species grew continuously (although never exceeding that on site A). The proposed hypothesis regarding the number of species seems correct, although it requires more evidence.

Dominant species

At the site with preserved soil the permanently dominant species was *Vaccinium myrtillus*, replaced only once by *V. vitis-idaea*. The latter dominated in the site with burnt soil for the first seven years; then it was replaced by *Calluna vulgaris*. Overall, that pattern corresponds to the idea that more damaged site dominance will be less stable. As shown in other works (LAMPAINEN et al. 2004), areas where *Vaccinium myrtillus* is dominant usually have higher regeneration rates and fewer tree seedlings.

Multivariate analyses

There was a clear trend in the succession patterns at both sites: they can be represented as imaginary lines on the principal component analysis plot based on species composition (Fig. 4). The lines ('trajectories' along which sites are 'moving' through the years) diverged along the first component, which means that different levels of damage caused the vegetation at the sites to develop differently, at least during the observed period. As mentioned above, the difference cannot be simply contributed to incidental causes due to the similarities between the initial sites and the control sites from the same group. Abundances of *Ledum palustre*, *Pohlia nutans* and *Equisetum sylvaticum* (all characteristic of site A) were most influential in the divergence along the first component; the second component gradually changed in the same direction for both sites and can represent the general characteristics of succession that do not differ; this description corresponds with the abundances of lingonberry and fireweed.

Cluster analysis divided plants into groups according to the site they preferred and to the impact they had on that site (Fig. 5). This claim is true in respect to *Pinus sylvestris* and *Calluna vulgaris*, which preferred the dryer and less competitive site B, and in respect to *Equisetum sylvaticum* and *Ledum palustre* which grew in the more humid site A but did not become dominant there.

Vaccinium myrtillus, *V. vitis-idaea* and *Pohlia nutans* constitute a group separate from all other plants: they were present at both sites and covered a significant area. This group contributed

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to similarities in development described by the second component, while other groups were responsible for the differences. The presence of *Populus tremula* on both sites did not seem to have a considerable effect on the succession pattern.

The data describing twelve-year-long succession patterns on Oleniy Island provides an insight into regeneration of northern pine forest. According to this information, such parameters as total projective cover and species composition can be considered reliable markers of the succession flow while others (such as dominant species and the total number of species) cannot qualify as such. Overall, the succession patterns on the more and less damaged sites had been diverging: the plant composition and abundance were far from similar.

Acknowledgements

All the field work was made during the White Sea Expedition of South-West High School (N1543) and was partly supported by the 'Sovremennoe estestvoznanie' foundation and Moscow institute of Open Education. We thank all members of the expedition and particularly Elena Kumskova, Andrey Kvashenko and Sergey Sukhov for their help in data collection. We are especially grateful to Elena Prozorova, Ekaterina Slobodkina, Daria Sukhova and Evgeniya Vorobyova, who not only helped on the field stage but were also involved in initial stages of data analysis and discussions.

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