THE BEETLE'S

How do bark-beetle outbreaks begin, how do they spread? What are the key factors that affect their population dynamics? Ongoing research has provided some understanding and knowledge, although many questions still remain to be answered fully.

Pavel Mezei, PhD
an expert on bark beetle physiology and ecology, has studied bark beetle outbreaks in Muránska Planina Forest and Tatra Mountains in Slovakia – some of the closest available analogies to the Białowieża ecosystem.

Dr. Pavel Mezei

Institute of Forest Ecology,
Slovak Academy of Sciences

The normal progression of forest dynamics involves the continuous replacement of tree cover, in a continual cycle, stretching back millions of years. There are various ways to model this – Korpel's model, for instance, posits three stages: a regeneration stage, old-growth stage, and senescence stage, together lasting approx. 300 years. In any case, whatever modeling is used, the consensus is the cycle generally ensures continuous forest cover: as one cycle is ending, the next is already underway and the soil is never without tree cover.

However, sometimes we can have a disturbance in the forest, when the tree cover is abruptly replaced by a single event. There are known as stand-replacing disturbances, and the recovery may proceed through what is known as gap dynamics or patch dynamics, when the forest is starting essentially from scratch. But even then, the tree layer is not entirely disrupted. Rather, it is quite quickly replaced for a time by pioneer species, then the forest gradually takes on an intermediate status, until eventually reverting to old-growth status. This is what occurs, for instance, after major windfalls or bark-beetle caused disturbances.

The bark beetle (more specifically, the Eurasian spruce bark beetle *Ips typographus*, which affects forests in Slovakia and Poland) infests trees by boring into the trunk, where the male creates a mating chamber and the females lay their eggs along the borings. Later the larvae feed on the phloem, in high-density populations they can circumvent the tree, causing the tree to die of starvation, as it becomes impossible to transport material from top to bottom of the tree.

The biology of the bark beetle is very well known, and it includes the stages of egg, larvae, pupae, then

DR. PAVEL MEZEI

SECRETS

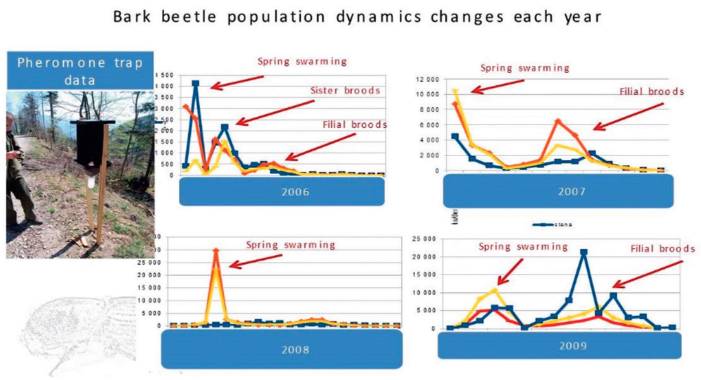
the yellow beetle, then adult. But its life-cycle involves one particular special feature: the possibility of more than one swarming in the course of a year. The females first lay their eggs in the spring, after which they may reemerge, make some regeneration feeding, then they lay another set of eggs – this is known as a "sister brood." Indeed, this can sometimes also recur one more time, involving a third egg-laying. And so, in the course of a single year, depending on conditions, we can have up to three different generations of bark beetle: the spring swarming (parental swarming), then sister broods, then filial broods.

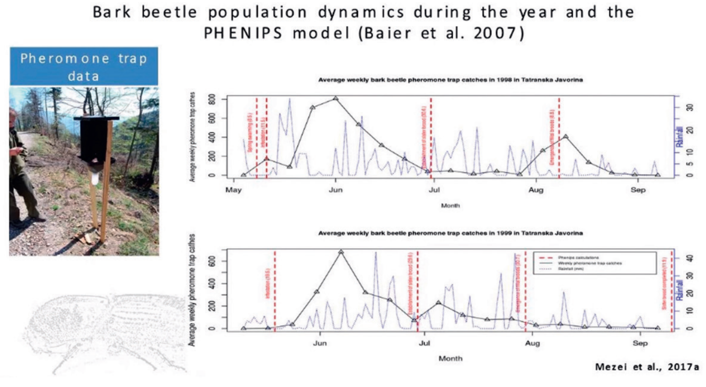
This can be demonstrated based on data from bark-beetle pheromone traps, as illustrated in Fig. 1. In 2006, for instance, the collected data shows how the bark beetles were able to infest the trees three times in one year. In 2008, on the other hand, when the summer was particularly cold and wet, so there was only one generation of the bark beetle. This is important for impact on the forest (although of course, we should also consider the numbers of beetles in each brood).

To be able to trace out the population dynamics, of course, we need to have reliable numerical data. There are various ways to gather such population data: these include pheromone traps (as seen in Fig. 1), tree mortality data, trap tree data, remote sensing techniques, and phenological models.

Figure 2. illustrates one such model and its verification in practice. The black line shows the bark beetle population dynamics from pheromone trap catches, whereas the blue line shows rainfall. The dashed red lines show the predictions of the PHENIPS model (Baier et al. 2007), which we can see can successfully anticipate the timing of the onset of the bark beetle generations (if they occur). Moreover, the juxtaposition of these data show how the population dynamics of the bark beetle is affected by the rain: then the spring swarming of 1998 was already underway but there was a rainy period, the spring swarming was halted for some time, but when the rain stop the bark beetle swarming continued.

If we look at longer-term data, such as tree mortality data stretching longer than 10 years in Fig. 3, it becomes possible to see longer term trends. This shows that a typical bark beetle outbreak has three phases: these are known as the incipient epidemic, epidemic, post-epidemic stages. An outbreak usually lasts from 3 to 7 years. The data in Fig. 3 is from the High Tatra Mountains, where we have data from the Polish side (TPN) and from the Slovak side (TANAP). The Polish side was not managed, whereas the Slovak side used various forest management strategies, but as the data show, both outbreaks ceased at the same time, showing similar dynamics.

1


2


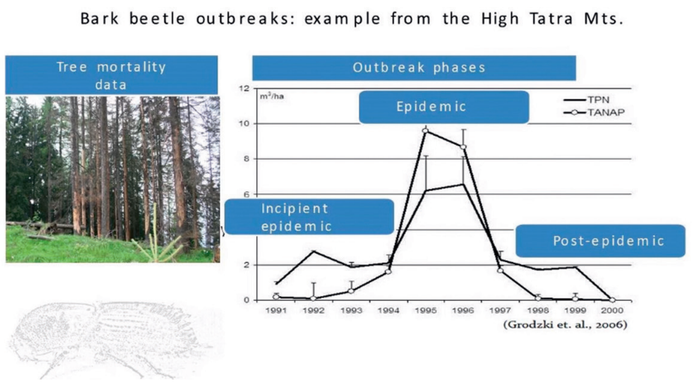
3


Fig. 1.
Bark beetle population dynamics in different years.

Fig. 2.
Bark beetle population dynamics over the course of a single year, juxtaposed against rainfall data and PHENIPS model (Baier et al. 2007) swarming predictions.

Fig. 3.
Example of bark beetle outbreak from High Tatra Mountains – both unmanaged Polish (TPN) and managed Slovak (TANAP) sides.

The bark beetle is what is known as an *r*-strategist organism: a small-body-size animal able to reproduce very quickly available resources present themselves. What factors influence the growth and then decline in bark beetle population dynamics? Some factors are dependent on the density of the bark beetles – the sex ratio, the interspecific competition, and available resources (at outbreak stages, the available resources somehow check the beetle population). Then density-independent factors: e.g. weather, altitude, climate, forest stand characteristics (often human controlled: age of trees, composition of forest).

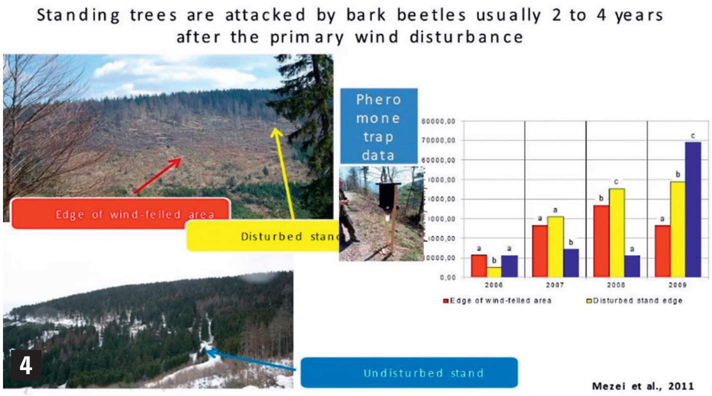
Which of these can be influenced by humans? We can for instance affect the sex ratio or intraspecific competition, but only to a limited extent – for instance by pheromone trapping, or trap trees. But such methods are tricky to use in practice, given that we never know in such cases what share of the population we have removed from the forest: while we can monitor the presence or remove some of the population, we never know objectively what the true extent of the population is. We cannot control the weather or altitude or climate (maybe we humans may change the climate, but not control it). We can, however, change the forest stand characteristics in a managed forest. Here of course there is a conflict, when the bark beetle reaches epidemic or outbreak levels, the forest becomes somehow bark-beetle-controlled, but on the other hand people want to control the forest too. In the vicinity of an outbreak we typically have both protected areas and managed forestes, but also something in between, called the buffer zone or conflict zone, and how to deal with it is usually a crucial strategic problem in forestry nature conservation.

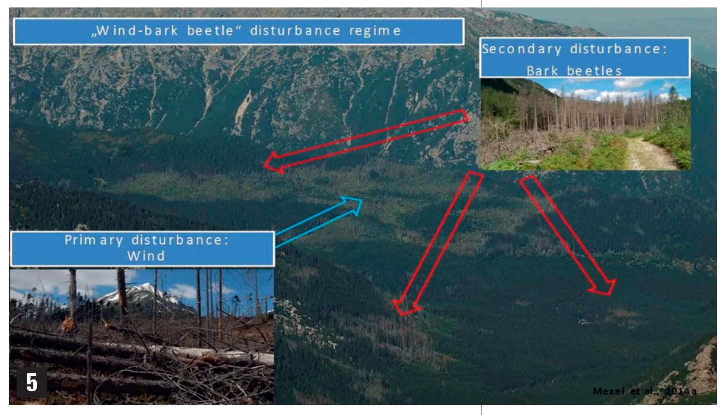
What has research taught us? Well, some factors affecting bark beetle population dynamics are well known, e.g. it is clear that forest stands under 50 years old are not attacked by the bark beetle (or at least, not by this particular species). At the start of an outbreak there is usually a disturbance event, which leads to a large volume of dead trees. Although standing trees cannot run or hide, they can still defend themselves against the bark beetle. But if we have an oversupply of dead trees, they lose their defensive mechanism immediately, and so become a very good substrate for bark beetle population development.

So, we talk about a combined wind and bark beetle disturbance regime. This is because usually we typically have a primary disturbance, which is caused by wind, and then after the bark beetles build up their population in this area they begin to attack the surrounding forest. The question is now long it takes the bark beetle to move from such a wind-felled forest into the surrounding disturbed forest, and then the surrounding undisturbed forest.

Research on this question, as illustrated in Fig. 4, has shown that standing trees are attacked by bark beetles usually 2 to 4 years after a primary wind disturbance. In the areas closest to the wind disturbance (the red lines), the bark beetle numbers were rising for a few years, but then started to decline. The surrounding disturbed standage (the yellow lines) remained attractive to the bark beetles the whole time. As for the surrounding undisturbed standage (the blue lines), the strong attack essentially began in the fourth year, interestingly, just as numbers in the original wind-felled areas are beginning to decline.

The conclusion is that we have from two to four years before the beetles begin to swarm from the area of the original disturbance into wholly new ar-





eas, usually creating a spatial-temporal pattern of infested trees. Of course, we cannot predict where the next patch of infestation will be, but research has shown that nearly all new attacks are within a distance of 500 meters of old ones. This suggests a certain conclusion for the strategy for areas around protected areas: the buffer zones surrounding them should be at least 500 meters wide in order to be effective as buffers.

Next, we also know something about the factors affecting tree mortality in spot initiation and spot spreading. For instance, most of the trees in newly initiated patches are older than 100 years and have DBH (diameter at breast height) of above 30 centimeters. Also, at the beginning of an outbreak most of the newly infested trees occurred in the lower-elevation forests, then in the middle of an epidemic the beetles begin to move to higher-elevations (given that resources are probably depleted in the lower-elevation areas), and in the post-epidemic phrase most of the attacks occurred in higher-elevation areas.

In terms of factors related to climate, it seems that bark beetle outbreaks require both a windfall event to initiate them, as well as favorable climactic conditions, conducive to the occurrence of sister broods. Warmer summer temperatures, for instance, and less rainy conditions are generally conducive to beetle outbreaks. This might indicate that given global warming we should expect more frequent bark beetle outbreaks in the future, but some recent findings suggest that there is a limit to the conducive influence of temperature, beyond which higher temperatures may actually have an inhibitory effect (making tree trunks too hot or too dry for infestation.

In terms of factors related to forest stand management strategies, there is still much research to be done. Bark-beetle-caused tree mortality rates initiated by windfalls tend to first increase, then decrease. The strategy of leaving bark-beetle-infested trees in the forest leads to strong growth in tree mortality, followed by a slow decline (as after a certain point, in subsequent years, given the huge amount of infested trees, there are few new trees to attack). The strategy of sanitary cutting, perhaps counterintuitively, has surprisingly also been found contribute to higher tree mortality in the next year, too, possibly because of the buffer-zone effect. And lastly, as for long-term sanitary management, cumulative sanitary cutting, this contributed to the decline of tree mortality, but there were cases when the whole forests were entirely harvested. From the ecological standpoint, this extreme result is not good.

So, in conclusion, one of our most important pieces of knowledge gleaned from research is that it takes 2 to 4 vegetation seasons for a windfall event to lead to a bark-beetle outbreak, providing time which might be used for preventative measures. The proper zonation of managed and unmanaged forest zones, and the actual impact of forest management strategies in the managed zones once an outbreak is imminent or underway, however, remain the subject of complex research.

Overall, taking the broader perspective, the 10-year cycle of a bark-beetle outbreak cycle is not that long when viewed in terms of the approx. 300-year forest regeneration cycle mentioned. The issue of bark beetles in the core zone may be seen as one of natural regeneration, and in the mountainous forests of Central Europe the dead trees are a suitable substrate for regeneration, but only after 20–30 years. So in the core zone it is necessary to leave the forest unattended, but the buffer zones may present a more complex problem.

Pavel Mezei

This is a summary of a presentation given by Dr. Mezei at the international conference "Managing the Bark Beetle Outbreak in the Białowieża Primeval Forest," organized by the Polish Academy of Sciences on 4 December 2017 (preceded by a study visit to Białowieża).

Fig. 4.
"Wind and bark beetle" disturbance regime.

Fig. 5.
Progression of bark beetle infestation from primary wind-felled area, to wind-disturbed stands, to wind-unaffected, standing trees.