



# Assessment of the mixed coniferous-broadleaved forest canopy disturbance induced by typhoon Maysak (2020) using drone-borne images near Vladivostok, Russia

Violetta D. Dziziuropa<sup>1\*</sup>, Kirill A. Korznikov<sup>1</sup>, Tatiana Y. Petrenko<sup>1</sup>, Sergey V. Dudov<sup>2</sup> & Pavel V. Krestov<sup>1</sup>

Violetta D. Dziziuropa<sup>1\*</sup>  
e-mail: dziziuropa.vd@mail.ru

Kirill A. Korznikov<sup>1</sup>  
e-mail: korzki@mail.ru

Tatiana Y. Petrenko<sup>1</sup>  
e-mail: petrenkotya@gmail.com

Sergey V. Dudov<sup>2</sup>  
e-mail: serg.dudov@gmail.com

Pavel V. Krestov<sup>1</sup>  
e-mail: krestov@botsad.ru

<sup>1</sup> Botanical Garden-Institute FEB RAS, Vladivostok, Russia

<sup>2</sup> Lomonosov Moscow State University, Moscow, Russia

\* corresponding author

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## ABSTRACT

We assess the impact of typhoon Maysak (2020) on the canopy structure of mixed coniferous-broadleaved forests with *Abies holophylla*, *Pinus koraiensis* and a complex of deciduous broad-leaved species and secondary oak forests of *Quercus mongolica*. The study was conducted in the experimental forest of the Botanical Garden-Institute FEB RAS. We classified the natural forest vegetation of the study area, created a high-resolution vegetation map, and assessed the damage from typhoon Maysak remotely using the ultra-high resolution images, obtained with an unmanned aerial vehicle. We found that the largest number and area of canopy gaps are associated with the conditionally primary coniferous-broadleaved forests, where *Abies holophylla* and *Pinus koraiensis* form the main canopy layer. The smallest number and area of gaps relate to the secondary oak forests.

**Keywords:** typhoon, tropical cyclone, canopy gap, unmanned aerial vehicle, forest disturbance, Primorye Region, *Abies holophylla*, *Pinus koraiensis*, *Quercus mongolica*

## РЕЗЮМЕ

Дзизюрова В.Д., Корзников К.А., Петренко Т.Я., Дудов С.В., Крестов П.В. Оценка нарушения полога смешанного хвойно-широколиственного леса, вызванного тайфуном "Майсак" (2020), с помощью снимков с беспилотника вблизи Владивостока, Россия. Оценено влияние тайфуна Майсак (2020 г.) на структуру основных типов лесной растительности, характерных для Южного Приморья (Россия), хвойно-широколиственных лесов с *Abies holophylla*, *Pinus koraiensis* с комплексом листопадных широколиственных видов и вторичных дубовых лесов (*Quercus mongolica*). Исследования проводились в экспериментальном лесном участке Ботанического сада-института ДВО РАН. Мы классифицировали естественную растительность исследуемой территории, создали крупномасштабную геоботаническую карту и оценили повреждения лесного полога от тайфуна Майсак по снимкам сверхвысокого разрешения, полученным с помощью беспилотного летательного аппарата. Выявлено, что наибольшее число и площадь ветровальных окон приурочены к условно первичным зональным хвойно-широколиственным лесам, где *Abies holophylla* и *Pinus koraiensis* формируют верхний полог. Меньшее число и площадь окон в пологе характерно для вторичных дубовых лесов.

**Ключевые слова:** тайфун, тропический циклон, окно в пологе, БПЛА, Приморский край, *Abies holophylla*, *Pinus koraiensis*, *Quercus mongolica*

Northeast Asia is increasingly influenced by tropical cyclones arriving from the equatorial Pacific (Altman et al. 2018, Korznikov et al. 2022). Tropical cyclones, called "typhoons" in West Pacific, having been preliminarily transformed on the polar front arrive in the mainland territory (Petrov et al. 2019). Depending on the kind of transformation, typhoons can cause heavy rains, strong winds, and catastrophic floods. With global climate change, typhoons began to move to northern latitudes, and their frequency and severity increased significantly over the past 50 years (Altman et al. 2018, Janda et al. 2021). Nowadays, typhoons cause disturbances in temperate and boreal forests, which were rarely affected by tropical cyclones in the past (Korznikov et al. 2022).

On 03.09.2020, typhoon Maysak passed over the south of Primorye Region with wind gusts up to 43 m/s. The

typhoon led to severe forest disturbances. It affected the Manchurian fir–Korean pine mixed forests dominated by *Abies holophylla* Maxim., *Pinus koraiensis* Siebold & Zucc. and several broad-leaved deciduous species, which are rated as rare and subject to protection (Krestov & Verkholat 2003). Such forests represent one of the most diverse vegetation types in the north temperate zone worldwide (Krestov et al. 2006). Currently, they are severely disturbed by fires in the whole range and replaced by low-productive communities of Mongolian oak (*Quercus mongolica* Fisch. ex Ledeb.) (OF – oak forest) in most of their range (Dobrynin 2000). Primary Manchurian fir–Korean pine mixed forests (FPMF – fir–pine mixed forests) survived in very small areas due to strict protection in the Kedrovaya Pad' Nature Reserve (central point 43.083333°N 131.5°E), Ussuri Nature Reserve (43.683333°N 132.55°E), and in the forest

area of the Botanical Garden-Institute FEB RAS (BGI) in Vladivostok (43.216667°N 131.983333°E) (Krestov et al. 2010). Typhoon Maysak affected all these areas.

The natural dynamics of mixed forests are characterized by periodic deaths of old trees due to windfalls and windbreaks (Omelko et al. 2018). The resulting treefall gaps, and canopy openings caused by the death of one or more trees, are important for forest development by affecting nutrient cycling and creating new niches, thereby helping to maintain a high level of biodiversity (Smirnova 2004). Studies in the boreal forests of Scandinavia and Russia, as well as in the montane boreal forests of Japan and North America, show that the disturbance regime largely determines forest structure and processes (McCarthy 2001). However, after a typhoon, an extremely large number of trees fall forming very large gaps, and wood waste accumulates, which can lead to pest infestation and increase the probability of fire (Marler 2013).

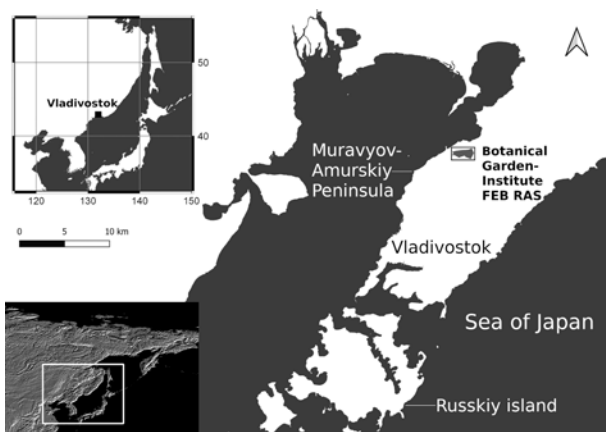
Gap size is one of the most important characteristics to record because it strongly influences vegetation growth and nutrient cycling (Schliemann & Bockheim 2011). Traditionally, the areas and shapes of the gaps are determined from detailed field measurements. However, this is laborious work resulting in relatively low data quality. The remote sensing techniques with an unmanned aerial vehicle (UAV) makes it possible to conduct a detailed and quick assessment of disturbances in the forest canopy, to assess the size and shape of the gaps.

The objective of this study is to assess the scale of the gaps formed as a result of typhoon Maysak in Manchurian fir-Korean pine mixed forests and secondary Mongolian oak forests, using remote sensing with UAV. The forest area of the BGI was used as a model for the forests under study, where the high-resolution inventory of vegetation was carried out shortly before the typhoon.

## MATERIAL AND METHODS

### Study area

The study area (Fig. 1) has a typical monsoon climate, which determines high humidity, moderate temperatures in summer and cold dry weather in winter. The annual temperature at the Vladivostok weather station is 4.9°C, and the



**Figure 1** Location of study area – the Botanical Garden-Institute FEB RAS, Vladivostok, Russia

mean monthly temperatures range from -12.3°C (January) to 19.8°C (August). The annual relative humidity is 71 %, and the annual precipitation is 860 mm, most of which falls in July and August. The territory of the BGI (169.7 hectares) is the federal significant specially protected natural area in the suburbs of the Vladivostok agglomeration. From the west to the east, the Central Ridge crosses the area. The steepness of the slopes ranges from 5° to 40.5°. The southern slope is short and steep (>20°). The maximum altitude is 170 m above sea level; the minimum is 20 m (Bulakh et al. 2010, Pogorelov et al. 2018). The mountainous terrain, heterogeneity of soil-ground and hydrological conditions, and the influence of anthropogenic factors determine the high diversity of natural flora and forest vegetation. The natural flora of vascular plants (excluding artificial sites) accounts for 604 species (Marchuk et al. 2022).

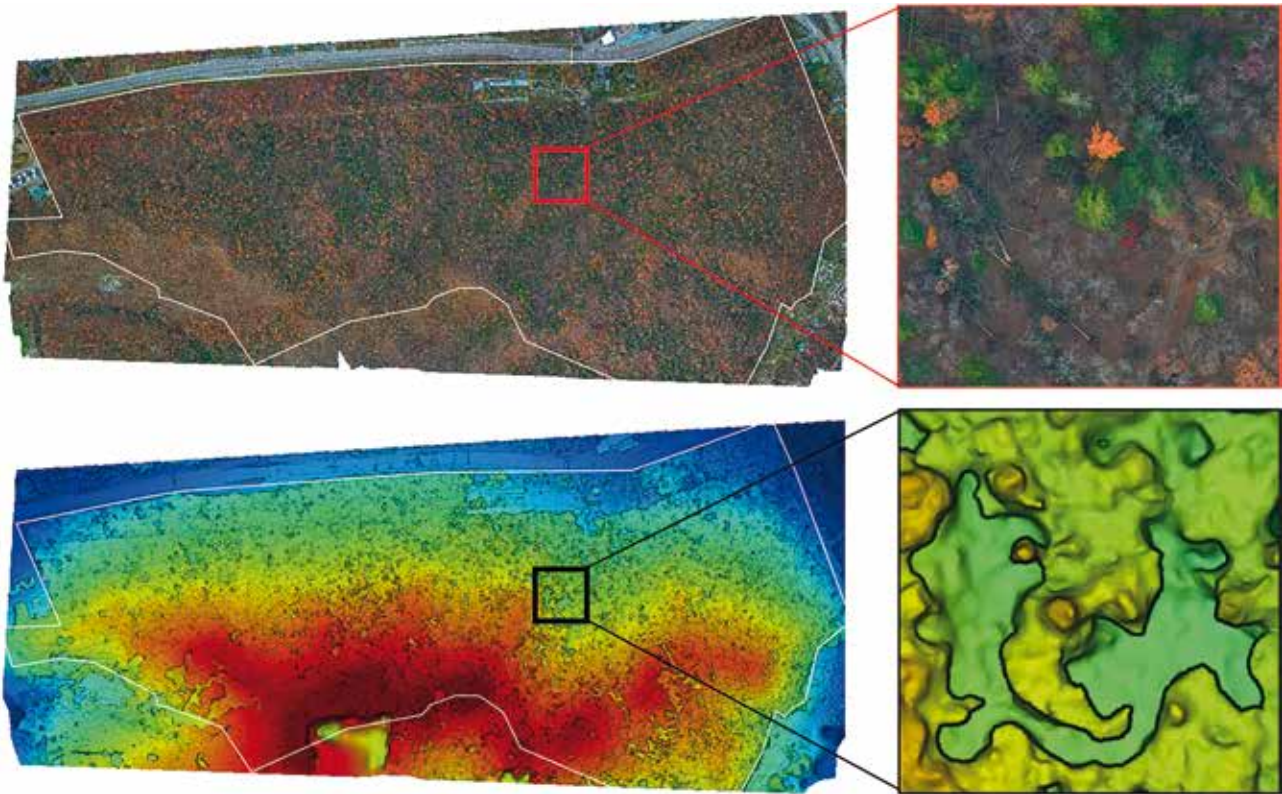
### Forest vegetation diversity

During the fieldwork, in August 2020, the forest area of the BGI was covered with a network of quadrat sample plots (400 m<sup>2</sup>) with a mesh of approximately 200 m. We recorded all vascular plant species and determined their cover according to the old seven-point Braun-Blanquet scale (Van der Maarel 1979), a number of vertical layers (upper, medium, and low tree layers, high (> 1 m), and low (< 1 m) shrub layers and grass layer). 23 relevés were made. Undergrowth and lianas were classified into the shrub or herb layers depending on their height. Tree heights were determined with a geodesic eclimeter. Plant species were identified with an aid of the floral guides by Kharkevich (1985–1996), Vorobyov (1982), Voroshilov (1982), and named in accordance with the Plants of the World Online botanical nomenclature database (<http://www.plantsoftheworldonline.org/>). The numerical vegetation classification was performed in the JUICE 7.0 software (Tichý 2002) using the Modified TWINSPAN algorithm (Roleček et al. 2009) with the clustering parameters: pseudo-species cut level – 5; thresholds 0, 5, 10, 25, 75; minimum group size – 2; given number of clusters – 4; a measure of Whittaker's beta diversity.

We made a map of the main vegetation types in QGIS 3.10 software environment (<https://qgis.org/>). To create the map, we covered the study area with a hexagonal grid (Birch et al. 2007) with a radius of the circumscribed circle of a hexagon equal to 25 m. Then we classified the cells based on the vegetation classification results and data received from the UAV. We manually recognized vegetation types on the ultra-high resolution raster (7 cm/pixel) obtained using a DJI Mavic 2 Pro quadcopter. We made all area calculations on the hexagonal grid, and then smoothened the boundaries of the sections.

### Forest gap measurement

We assessed the disturbance from typhoon Maysak remotely using the ultra-high resolution images (7 cm/pixel), obtained with the UAV. Based on them, we created an orthophotomosaic of forest cover and a raster with relative heights (elevation raster) in the Drone Deploy program (<https://www.dronedeploy.com/>) (Fig. 2). We combined



**Figure 2** Forest cover raster and the relative height raster used to define the boundaries of canopy gaps

the elevation raster, which reflects local depressions in forest canopy gaps, and the forest cover raster, which shows trunks of fallen trees. As gaps formed by typhoon Maysak, we considered these depressions on the elevation layer, next to which lying trees were found. We manually outlined their boundaries in the QGIS 3.10 program. The gap areas were also calculated in QGIS 3.10.

## RESULTS

### Forest vegetation diversity

As a result of the BGI forest vegetation numerical classification, all relevés were grouped into four clusters that can be recognized in the orthophoto image: two clusters represent the FPMF, one cluster – the OF, and one – the poplar and willow early successional stands, growing on wet sites along the forest road.

The main difference between the two types of FPMF is in the ontogenetic spectra of *Abies holophylla* and *Pinus koraiensis*. We call the first type "conditionally primary", and the second – "transformed". In the first case, forests include all stages of the pre-generative and generative periods of trees; juvenile and adult plants predominate. *A. holophylla* and *P. koraiensis* are dominants in the forest canopy. In the second case, these two species occur mainly under the canopy and are abundant in the undergrowth; immature and juvenile plants predominate. The canopy in this case is dominated by broadleaved deciduous species. The lower tree layer in both cases is formed by *Carpinus cordata* Blume. Transformed FPMFs are characterized by greater species richness. These two forest types can be interpreted as FPMF at different stages of succession.

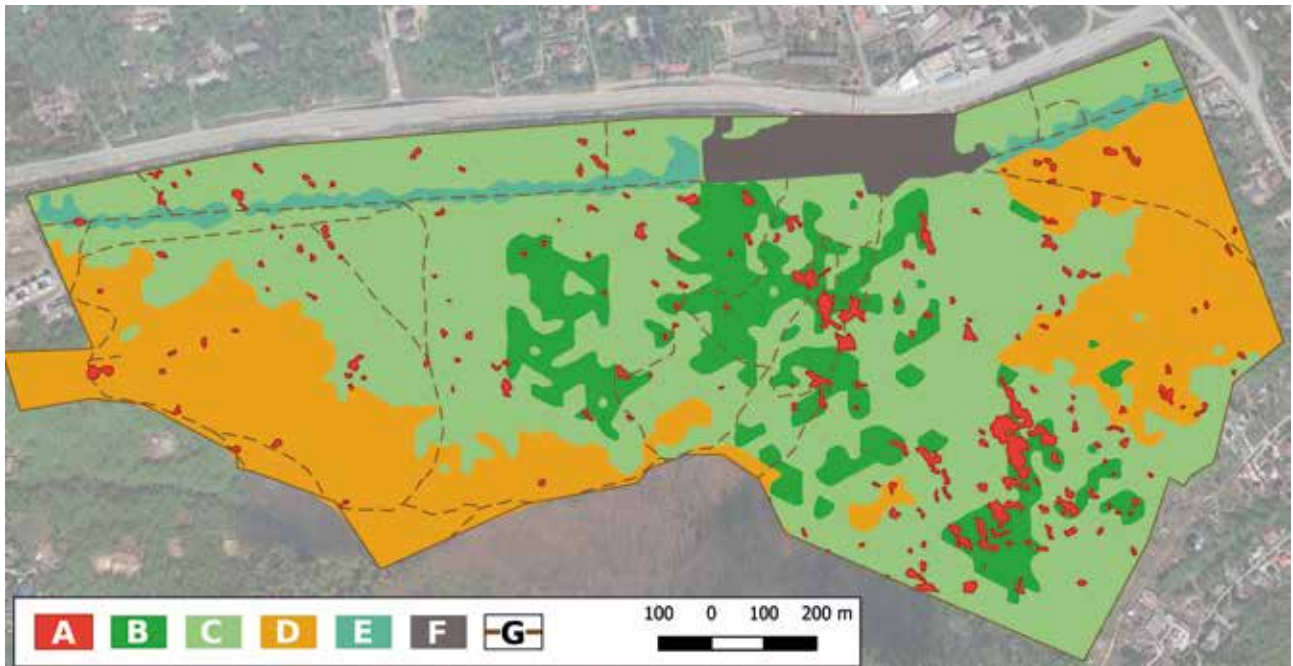
The third forest type represents OF with *Lespedeza bicolor* Turcz. in the undergrowth. *A. holophylla* and *P. koraiensis*, mainly juvenile, are rare, but their presence confirms that FPMF can recover from secondary OF in case of absence of fires (Kudinov et al. 2007). This is confirmed by the common diagnostic species for the three groups: *A. holophylla*, *Q. mongolica*, *Acer mono* Maxim., *Acer pseudosieboldianum* (Pax) Kom., *Sorbus alnifolia* (Siebold & Zucc.) K.Koch. (Table 1).

The fourth type of forest is the secondary poplar-willow stands (*Populus maximowiczii* A. Henry, *Salix* spp.), which arose as a result of human activity, and therefore we did not consider their features here. The following are the characteristics of natural forests of the BGI territory (Table 1, synoptic table – Appendix 1 Table 2).

Four vegetation groups were mapped (Fig. 3). The conditionally primary FPMF has been preserved in the central and eastern parts of the BGI forest territory. Transformed FPMF occupy most of the forest territory. OF are confined to the southern and western slopes, and early successional poplar and willow stands stretch in a narrow strip along the roads with the drainage ditch.

### Canopy gap structure

The total area of canopy disturbances in the BGI forests due to typhoon Maysak is 45 300 m<sup>2</sup> (equal to 3 % of the study area). Most of the gaps are of elongated shape stretched from the northwest to the southeast. The average gap size is  $228.8 \pm 32.6$  m<sup>2</sup> (n=198, the median value is 119 m<sup>2</sup>). On average, one fallen tree accounts for  $109.2 \pm 4.5$  m<sup>2</sup>, (median value is 98), and this area does not statistically change from the number of jointly felled trees (p-value 0.475) (Fig. 4).



**Figure 3** Large-scale vegetation map of the Botanical Garden-Institute FEB RAS and typhoon Maysak disturbances. A – canopy gaps; B – conditionally primary Manchurian fir–Korean pine mixed forests; C – transformed mixed forests; D – Mongolian oak forests; E – poplar and willow artificial stands; F – non-forest areas; G – paths

**Table 1.** Main stand parameters (with means in parentheses) of the Manchurian fir-Korean pine mixed forests and the Mongolian oak forests of the Botanical Garden-Institute FEB RAS

Stand parameter / Species	Conditionally primary mixed forests	Transformed mixed forests	Mongolian oak forests
Number of relevés	7	10	6
Area, m <sup>2</sup>	223 934	89.36	45.53
Aspect	NW, N, NE	NW, N, NE	W, SW, S, SE
Slope, %	0–15	3–30	20–25
Number of layers	4–6	5–6	3–5
Height of the canopy layer, m	20–30 (26.2)	19–29 (23.8)	15–16 (15.5)
Density of upper tree layer, %	10–35 (25)	20–55 (36)	20–45 (36)
Height of middle tree layer, m	6–18 (12.4)	9–18 (13.4)	Absent
Density of middle tree layer, %	40–65 (48.3)	10–65 (36.7)	Absent
Number of species in relevé	40–57 (49.3)	46–74 (59.6)	26–58 (37.8)
<b>Canopy diagnostic and dominant (*) species (Braun-Blanquet old scale)</b>			
<i>Abies holophylla</i>	2*	+	+
<i>Pinus koraiensis</i>	1*		
<i>Tilia amurensis</i>	1	2*	
<i>Quercus mongolica</i>	+	2*	3*
<i>Betula davurica</i>		1*	
<i>Kalopanax septemlobus</i>		1*	
<b>Subcanopy diagnostic species</b>			
<i>Ulmus laciniata</i>	+		
<i>Acer barbinerve</i>	1	+	
<i>Acer pseudosieboldianum</i>	1	+	
<i>Acer tegmentosum</i>	1	+	
<i>Carpinus cordata</i>	3	2	
<i>Eleutherococcus senticosus</i>	1	1	
<i>Philadelphus tenuifolius</i>	2	2	
<i>Schisandra chinensis</i>	1	+	
<i>Sorbus alnifolia</i>	+	+	+
<i>Acer mono</i>	+	+	+
<i>Corylus mandshurica</i>		+	
<i>Lespedeza bicolor</i>			2
<b>Herb layer diagnostic species</b>			
<i>Oxalis acetosella</i>	1		
<i>Maianthemum dilatatum</i>	r		
<i>Dryopteris crassirhizoma</i>	2	1	
<i>Hylomecon vernalis</i>	1	+	
<i>Prenanthes tatarinovi</i>	+	1	
<i>Thalictrum filamentosum</i>	1	+	
<i>Actaea asiatica</i>		1	
<i>Athyrium sinense</i>		+	
<i>Rabdosia excisa</i>		+	
<i>Carex lanceolata</i>			2
<i>Doellingeria scabra</i>			2
<i>Fragaria orientalis</i>			+
<i>Vicia unijuga</i>			1

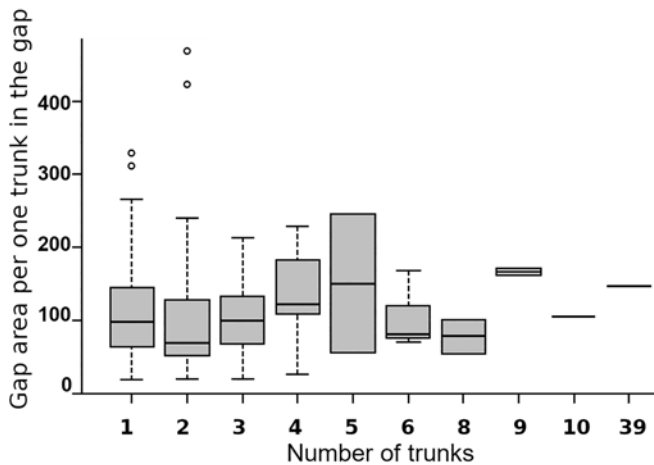
The total area of gaps in conditionally primary FPMF is 17 650 m<sup>2</sup> (equal to 8 % of the total forest type area), in disturbed FPMF – 21 406 m<sup>2</sup> (equal to 2.4 %). Many gaps are located at the border of these forest types; therefore, we consider the FPMF as an indivisible unit, which includes 158 gaps. The average gap size in the FPMF is 247.2 ± 40.3 m<sup>2</sup> (n = 158, the median is 118.5 m<sup>2</sup>); one gap is formed on average by 1–5 trees.

In total, 37 gaps are formed in OF. They cover 5901 m<sup>2</sup> (equal to 1.3 %). The average gap size in OF is 159.5 ± 24.4 m<sup>2</sup> (n = 37, median is 121 m<sup>2</sup>); most gaps appeared after falling 1–2 trees. There are only 3 gaps in the early successional poplar and willow stands with the total area 343 m<sup>2</sup> (equal to 0.6 %) (Fig. 5).

Most of the gaps were formed as a result of a single tree fall (121 gaps) or 2–4 fallen trees (64 gaps). 12 gaps were formed by 5–10 fallen trees. In addition, there was one major windfall patch resulting from the fall of 39 trees. This largest patch is located in the southeastern part of the study area in the conditionally primary FPMF and its area is 5 732 m<sup>2</sup>.

## DISCUSSION

The disturbances by typhoon Maysak in FPMF are greater compared with OF. The disturbances to the forest canopy are associated with conditionally primary FPMF. This can be explained by the loss of the tallest and oldest *A. holophylla* and *P. koraiensis* trees with above-canopy crowns. A similar situation was observed in the Odaesan National Park (Republic of Korea), when 85 % of the total *Abies nephrolepis* trees and 91 % of the

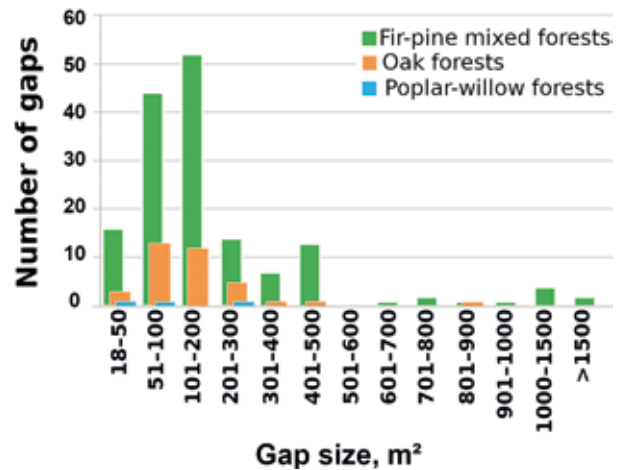


**Figure 4** The ratio of the gap per a tree ( $\text{m}^2$ ) and the number of fallen trees (median values and quartiles)

total *A. holophylla* trees in mixed forests fell due to strong winds in October 2006, but the Mongolian oak forests were disturbed significantly less (Jeon et al. 2015). Clinton & Baker (2000) demonstrated that large trees are more prone to falling because they act as masts in very windy conditions. Ruel et al. (2001) demonstrated that species with shallow root systems are especially vulnerable to high winds. Thus, *Abies* species are presumably susceptible to strong winds due to their high elevation and shallow root systems.

According to McCartney's (2001) worldwide forest gap study, the average gap size for single treefalls normally ranges from 50 to 200 ( $250 \text{ m}^2$ ). McCartney also pointed out median values of average gap size are highest for the temperate coniferous forests and southern hemisphere forests dominated by large-sized canopy trees. For temperate hardwood forests, a variation of average gap size is  $28\text{--}239 \text{ m}^2$  (median is  $79 \text{ m}^2$ ), and for temperate coniferous forests is  $77\text{--}131 \text{ m}^2$  (median is  $85 \text{ m}^2$ ) (McCartney 2001). Thus, the average size of the gaps formed by typhoon Maysak corresponds to the average size for single treefalls around the world. However, median gap sizes in FPMF and OF are higher than those reported in McCartney's review. This reflects the higher tree density and, correspondingly, narrower niches in the Far Eastern temperate forests compared to their analogs in Europe and North America.

The range values of gap fraction in temperate hardwood forests are  $2\text{--}20 \%$  (the median is  $10 \%$ ), and for temperate coniferous forests –  $11\text{--}18 \%$  (the median is  $4 \%$ ) (McCartney 2001). Thus, the area of disturbance of the forest stands in the BGI formed after typhoon Maysak can be estimated as within the normal range. However, in the territories of the south of Primorye Region, where areas covered with mixed forests are larger (the Kedrovaya Pad' Nature Reserve, etc.), we observed massive windblows and windthrows (our unpublished data, spring 2021). The fact that typhoons become a significant problem for the south of the Russian Far East is also evidenced by disturbances in southwest Sakhalin due to the tropical cyclone in 2015 (Korzni- kov et al. 2022) and in Sikhote-Alin Nature Reserve due to typhoon Lionrock in 2016 (Vozmishcheva et al. 2019), when  $9 \%$  of the forests turned into continuous windblows.



**Figure 5** Distribution of gaps by forest types

If the frequency or strength of typhoons increases in the future, many forests, including old growth forests, may gradually lose large trees. In addition, the ratio of coniferous species in forests recovered from the typhoon may change. According to the study of the felling area, the juvenile specimens of *A. holophylla* tolerate a sudden change in lighting quite well, while juvenile specimens of *P. koraiensis*, suddenly exposed to light from under the canopy, wilt and slow down in growth (Vasil'ev & Kolesnikov 1962). A study of the typhoon activity influence on the canopy accession strategies of *Abies nephrolepis*, *Pinus koraiensis*, and *Quercus mongolica*, based on long-term patterns of radial tree growth along a  $1500 \text{ km}$  latitudinal gradient of typhoon activity decline, showed that the typhoon activity gradient is an important indicator influencing changes in the life cycle traits of *P. koraiensis* and *Q. mongolica*, and not so important for the growth strategy of *A. nephrolepis* (Janda et al. 2021). Flexibility in growth strategies indicates that *P. koraiensis* and *Q. mongolica*, will be able to cope with shifts in disturbance patterns caused by poleward migration of typhoons and increased typhoon intensity. The ability of *A. holophylla* to adapt to these disturbances remains questionable.

The remote sensing with UAVs opens an opportunity to assess the disturbances in forests quickly and accurately. On the other hand, the method we propose has some components based on photointerpretation and, therefore, implementation for large areas may be time-consuming. Perhaps in the future, it will be convenient to apply machine learning to identify treefall gaps.

## CONCLUSION

Very high resolution orthophoto images obtained using UAVs made it possible to solve two important tasks in the study of protected forests: to make an accurate map of vegetation and to assess the degree of damage to the forest stand after the typhoon. We assessed the impact of typhoon Maysak damage on the Manchurian fir-Korean pine mixed forests and the secondary Mongolian oak forests in the BGI protected area, south of Primorye Region of Russia. The transformed FPMF occupies most of the BGI forest territory. The smaller area is occupied by conditionally primary FPMF and OF. The greatest disturbances to the forest canopy are

associated with conditionally primary FPMF (8 % of the total forest type area), where *A. holophylla* is included in the canopy. The composition and structure of vegetation cover may result not only from the environmental factors but also from large-scale or small-scale disturbances, the frequency of these events, and the ways in which territories recover from disturbances. If earlier the main type of disturbance in the FPMF was fires, then recently their importance has decreased, since these forests are found mainly in specially protected and hard-to-reach natural areas in humid conditions. Thus, gaps as a result of natural death and periodic typhoons can become the main disturbances that affect the structure of the Manchurian fir-Korean pine mixed forests in the south of Primorye Region of Russia.

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## LITERATURE CITED

- Altman, J., O.N. Ukhvatkina, A.M. Omelko, M. Macek, T. Plener, V. Pejcha, T. Cerny, P. Petrik, M. Srutek, J.-S. Song, A.A. Zhmerenetsky, A.S. Vozmishcheva, P.V. Krestov, T.Y. Petrenko, K. Treydte & J. Dolezal 2018. Poleward migration of the destructive effects of tropical cyclones during the 20th century. *Proceedings of the National Academy of Sciences* 115(45):11543–11548.
- Birch, C.P., S.P. Oom & J.A. Beecham 2007. Rectangular and hexagonal grids used for observation, experiment and simulation in ecology. *Ecological Modelling* 206(3–4):347–359.
- Brasfield & Gorrie. 2022. *Drone Mapping Software*. Drone Deploy. Available from <http://www.dronedeploy.com/>. Last accessed 12.06.2022.
- Bulakh, E.M., I.A. Galanina, V.A. Kostenko, V.A. Nechaev, B.S. Petropavlovsky, O.V. Khrapko & Yu. A. Chistyakov 2010. The nature phenomenon in Vladivostok. *Vestnik DVO RAN* 4:90–96 (in Russian). [Булах Е.М., Галанина И.А., Костенко В.А., Нечаев В.А., Петропавловский Б.С., Храпко О.В., Чистяков Ю.А. 2010. Природный феномен во Владивостоке // Вестник ДВО РАН. Вып. 4. С. 90–96].
- Clinton, B.D. & C.R. Baker 2000. Catastrophic windthrow in the southern Appalachians: characteristics of pits and mounds and initial vegetation responses. *Forest Ecology and Management* 126(1):51–60.
- Janda P., O.N. Ukhvatkina, A.S. Vozmishcheva, A.M. Omelko, J. Dolezal, P.V. Krestov, A.A. Zhmerenetsky, J.-S. Song & J. Altman 2021. Tree canopy accession strategy changes along the latitudinal gradient of temperate Northeast Asia. *Global Ecology and Biogeography* 30(3):738–748.
- Jeon, M., K. Lee & Y. Choung 2015. Gap formation and susceptible *Abies* trees to windthrow in the forests of Odaesan National Park. *Journal of Ecology and Environment* 38(2):175–183.
- Kharkevich, S.S. (editor-in-chief) 1985–1996. *Vascular Plants of the Soviet Far East. Vol. 1–8*. Nauka, Leningrad, (in Russian). [Сосудистые растения Советского Дальнего Востока / отв. ред. С.С. Харкевич. Ленинград: Наука. Т. 1–8].
- Korzniakov, K., D. Kislov, J. Dolezal, T. Petrenko & J. Altman 2022. Tropical cyclones moving into boreal forests: Relationships between disturbance areas and environmental drivers. *Science of The Total Environment*, 844: 156931.
- Krestov, P.V., D.I. Nazimova, N.V. Stepanov & D. DellaSala 2010. Humidity dependent forests of the Russian Far East, Inland Southern Siberia, and Korean Peninsula. In: *Temperate and Boreal Rain Forest of the World: Ecology and Conservation* (D. DellaSala, ed.), pp. 222–234, Island Press, New York.
- Krestov, P.V., J.-S. Song, Y. Nakamura & V.P. Verkhohat 2006. A phytosociological survey of the deciduous temperate forests of mainland Northeast Asia. *Phytocoenologia* 36(1): 77–150.
- Krestov, P.V. & V.P. Verkhohat 2003. *Rare plant communities of Primorye and Amur Region*. Institute of Biology and Soil Science FEB RAS, Vladivostok, 200 pp. (in Russian). [Крестов П.В., Верхолат В.П. 2003. Редкие растительные сообщества Приморья и Приамурья Владивосток: Биолого-почвен. ин-т ДВО РАН. 200 с.].
- Kudinov, A.I., Y.I. Manko, G.N. Butovets, G.A. Gladkova, E.V. Zhabyko, D.-K. Lee, H.-S. Kang & N. Batkhuu 2007. Features of the dynamics of virgin coniferous-deciduous forests of southern Primorye. *Lesovedenie* 3:11–22 (in Russian). [Кудинов А.И., Манько Ю.И., Бутовец Г.Н., Гладкова Г.А., Жабыко Е.В., Дон К.А., Канг Х.С., Батхуу Н. 2007. Особенности динамики девственных хвойно-широколиственных лесов Южного Приморья // Лесоведение. Вып. 3. С. 11–22].
- Marchuk, E.A., S.V. Nesterova, M.N. Koldaeva, V.A. Kalinkina, O.V. Khrapko & N.A. Tsarenko 2022. Flora of the protected territory of the Botanical Garden-Institute FEB RAS (Vladivostok, Russia). *Botanica Pacifica* 11(2):131–146.
- Marler, T.E. 2013. Increased threat of island endemic tree's extirpation via invasion-induced decline of intrinsic resistance to recurring tropical cyclones. *Communicative & Integrative Biology* 6(1):e22361.
- McCarthy, J. 2001. Gap dynamics of forest trees: a review with particular attention to boreal forests. *Environmental Reviews* 9(1): 1–59.
- Omelko, A., O. Ukhvatkina, A. Zhmerenetsky, L. Sibirina, T. Petrenko & M. Borovsky 2018. From young to adult trees: How spatial patterns of plants with different life strategies change during age development in an old-growth Korean pine-broadleaved forest. *Forest Ecology and Management* 411(1):46–66.
- Petrov, E.O., N.N. Sokolikhina & E.K. Semenov 2019. Transformation of tropical cyclones on the Polar front over the Primorsky kraj. *Russian Meteorology and Hydrology* 44(8):564–570.
- Pogorelov, A.R., I.S. Vovzhenyak & K.M. Korovin 2018. Landscape situation in the nature protection zone of the Vladivostok agglomeration. *Sotsialno-ecologicheskie tekhnologii* 1:65–78 (in Russian). [Погорелов А.Р., Вовзhenyak И.С., Коровин К.М. 2018. Ландшафтная ситуация в природоохранной зоне Владивостокской агломерации // Социально-экологические технологии. Вып. 1. С. 65–78].
- QGIS 2022. *QGIS: A free and open source geographic information system*. 2020. QGIS Homepage. Available from <https://qgis.org/en/site/>. Last accessed 12.06.2022.
- R Core Team 2017. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. Available from <https://www.Rproject.org/>. Last accessed 12.06.2022.
- Roleček, J., L. Tichý, D. Zelený & M. Chytrý 2009. Modified TWINSpan classification in which the hierarchy respects cluster heterogeneity. *Journal of Vegetation Science* 20(4):596–602.

- Ruel, J.C., D. Pin & K. Cooper 2001. Windthrow in riparian buffer strips: effect of wind exposure, thinning and strip width. *Forest Ecology and Management* 143(1–3):105–113.
- Schliemann, S.A. & J.G. Bockheim 2011. Methods for studying treefall gaps: a review. *Forest Ecology and Management* 261(7):1143–1151.
- Smirnova, O.V. 2004. *East European forests: history in the Holocene and the present*. Nauka, Moscow, 498 pp. (in Russian). [Смирнова О.В. 2004. Восточно-европейские леса: история в голоцене и современность. Москва: Наука. 498 с.].
- Tichy, L. 2002. JUICE, software for vegetation classification. *Journal of Vegetation Science* 13(3): 451–453.
- Van der Maarel, E. 1979. Transformation of cover-abundance values in phytosociology and its effects on community similarity. *Vegetatio* 39(2):97–114.
- Vasiliev, N.G. & B.P. Kolesnikov 1962. *Manchurian fir mixed forests of south of Primorye*. Nauka, Moscow, 149 pp. (in Russian). [Васильев Н.Г., Колесников Б.П. 1962. Чернопихово-широколиственные леса Южного Приморья. Москва: Наука, 149 с.].
- Vorobiev, D.P. 1982. *Keys to vascular plants in the vicinity of Vladivostok*. Nauka, Leningrad, 254 pp. (in Russian). [Воробьев Д.П. 1982. Определитель сосудистых растений окрестностей Владивостока. Ленинград: Наука, 254 с.].
- Voroshilov, V. N. 1982. *Keys to plants of the Soviet Far East*. Nauka, Moscow, 672 pp. (in Russian). [Ворошилов В.Н. 1982. Определитель растений советского Дальнего Востока. Москва: Наука, 672 с.].
- Vozmishcheva, A.S., S.N. Bondarchuk, M.N. Gromyko, D.E. Kislov, E.A. Pimenova, M.A. Salo & K.A. Korznikov 2019. Strong disturbance impact of tropical cyclone Lionrock (2016) on Korean pine–broadleaved forest in the middle Sikhote-Alin mountain range, Russian Far East. *Forests* 10:1017.