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# Fire severity and tree size affect post-fire survival of Afrotropical forest trees

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## Abstract

**Background:** Fire is recognized as an important factor in determining the distribution and composition of Southern Cape Afrotropical Forest in South Africa, although comprehensive understanding of the resilience of these forests to fire is lacking. We investigated effects of fire severity and tree size on post-fire survival of Afrotropical forest tree species.

**Results:** Fire severity was estimated from observed damage to the main stem of trees, and trees were considered to have survived if they resprouted from the main stem or had green foliage in the canopy. A total of 88 plots, 40 species, and 1 378 trees were surveyed 19–24 months post-fire. We assessed the survival response of all trees collectively and for 10 species (with sample size > 40) individually, using logistic regression. Relative to other forests of the world, the post-fire survival rate (45%) of Afrotropical forest trees collectively was comparable to that in coniferous and tropical forests but lower than that in other temperate forests and in neighboring dune thicket. Fire severity had a significant negative effect on survival and tree size had a significant positive effect. Total variance explained by the model (for species collectively) was 40.8%, of which fire severity and tree size combined explained 13.2%, and species as random factor, 27.6%. Respective tree species showed differential survival responses—four species showed high survival (> 60%), while five species showed low survival (< 40%). Further, some species exhibited strong resprouting from the base or main stem while others rarely resprouted. The survival response and resprouting abilities of species which occur in both Afrotropical forest and neighboring, more fire-exposed dune thicket, were generally poorer in forest. Such discrepancies imply that historical fire regimes associated with vegetation types likely drive species adaptations.

**Conclusions:** Our findings suggest that fire severity and fire frequency (in terms of how tree size relates to fire frequency) are important for maintaining species richness and diversity within and between forest types. Varying resilience to fire among species supports previous assertions that fire affects species composition and diversity in these forests and suggests that potential changes in fire regimes due to global change will have consequences for forest conservation.

**Keywords:** Afrotropical forest, Fire intensity, Fire severity, Large scale disturbance, Resilience, Resprouting, South Africa, Tree mortality, Tree size, Wildfire

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## Resumen

**Antecedentes:** El fuego es reconocido como un factor importante en la determinación de la distribución y composición de los bosques Afrotemplados del Sur del Cabo en Sudáfrica, aunque el entendimiento comprensivo de la resiliencia de este bosque al fuego es nula. Investigamos los efectos de la severidad del fuego y el tamaño de los árboles en la supervivencia post fuego de las especies de árboles en estos bosques Afrotemplados.

**Resultados:** La severidad del fuego fue estimada de la observación del daño al tallo principal de los árboles, y estos árboles fueron considerados como sobrevivientes si ellos rebrotaban desde su tallo principal o presentaban follaje verde en su dosel. Un total de 88 parcelas, 40 especies y 1.378 árboles fueron relevados entre los 19 y 24 meses post fuego. Determinamos la respuesta a la supervivencia de todos los árboles colectivamente, y para 10 especies (con un tamaño de muestra > 40 individuos) usando regresiones logísticas. Relacionado con otros bosques del mundo, la tasa de supervivencia post fuego (45%) de los árboles de este bosque considerados colectivamente, fue comparable a aquellos de bosques de coníferas y tropicales, pero menores que en otros bosques templados y en matorrales de dunas vecinos. La severidad del fuego tuvo un efecto negativo significativo en la supervivencia, mientras que el tamaño de los árboles tuvo un efecto significativo positivo. La varianza total explicada por el modelo (para las especies de manera colectiva) fue 40,8%, de la cual la combinación de la severidad del fuego con el tamaño de los árboles explicó el 13% e los casos, y las especies como factor aleatorio el 27,6%. Las respectivas especies de árboles mostraron sobrevivencias diferenciales; cuatro especies mostraron una alta supervivencia (> 60%), mientras que cinco especies mostraron una baja supervivencia (40%). Además, algunas especies exhibieron una alta tasa de rebrote desde la base o del tallo principal, mientras que otras raramente rebrotaron. La respuesta a la supervivencia y las habilidades de rebrotar de especies que ocurren en los bosques Afrotemplados y en los matorrales de dunas adyacentes, más expuestos al fuego, fueron generalmente más pobres en el caso de los bosques. Estas discrepancias implican que los regímenes históricos de fuego asociados a tipos de vegetación probablemente conduzcan a la adaptación de las especies.

**Conclusiones:** Nuestros resultados sugieren que la severidad del fuego y su frecuencia (en términos de cómo el tamaño de los árboles se relaciona con la frecuencia del fuego) son importantes para mantener la riqueza de especies y diversidad dentro y entre, distintos tipos forestales. La variación de la resiliencia al fuego entre especies confirma aseveraciones previas de que el fuego afecta la composición y diversidad en esos bosques, y sugiere que los cambios potenciales en los regímenes de fuego debidos al cambio climático global tendrán consecuencias en la conservación de los bosques.

## Background

Indigenous forest in South Africa covers around 300,000 ha or 0.1% of the land surface area (Rutherford and Westfall 1994). Southern Cape Afrotemperate Forest (hereafter “Afrotemperate forest”) is the largest closed-canopy forest complex in Southern Africa covering an area of 60 560 ha (Geldenhuys 1991; Mucina and Geldenhuys 2006). Most Afrotemperate forest patches are < 100 ha (Low and Rebelo 1996), but the largest single patch is located in the southern Cape of South Africa near the town of Knysna and is 25,706 ha in size (Geldenhuys 1991). Fire is a natural disturbance agent in the region and maintains the distribution of Afrotemperate forest patches within its potential range (Geldenhuys 1994). Afrotemperate forest patches are located within a matrix of flammable fynbos shrubland, although these forest patches seldom burn due to their position in the landscape (Geldenhuys 1994), live foliar moisture content and fuel structure (van Wilgen et al. 1990). However, under certain climatic conditions Afrotemperate forest patches are susceptible to fire mostly spreading from the adjacent fynbos or invasive alien *Pinus* plantations into the margins of forest patches (Geldenhuys 1994; Watson

and Cameron 2001; Giddey et al. 2021). Drought disturbs the micro-climate of Afrotemperate forest by desiccating the available fuel, increasing flammability and allowing fire to enter (Archibald et al. 2009). Fire thus maintains the boundary between Afrotemperate forest and fynbos, with the ecotone in a constant state of flux (Geldenhuys 1994; Schmidt and Vlok 2002). During periods between long fire return intervals, Afrotemperate forest expands into fynbos (Luger and Moll 1993; Everard 1986), while frequent high intensity fires are thought to cause Afrotemperate forest patches to retract and fynbos to expand (Geldenhuys 1989; Watson and Cameron 2001; Schmidt and Vlok 2002). Contemporary climate of the southern Cape region is drier than the more mesic conditions that promoted the expansion of forest during the late Holocene (ca. 2500 years BP) (Martin 1968). Furthermore, recent increases in high fire danger weather conditions are likely to contribute to an increase in fire frequency and severity (Kraaij et al. 2013a) potentially making forests more vulnerable to fire.

Mature Afrotemperate forest has a defined structure of woody vegetation consisting of an emergent layer, canopy layer, sub-canopy layer, and understory (Seifert

et al. 2014), with an average canopy height of 20 m to 25 m (Geldenhuys and van Laar 1980). Afrotropical forest canopy species are trees with a dominant or codominant position in the canopy of mature forest (Geldenhuys 1989) and play a vital role in maintaining a closed canopy structure, canopy height, and subsequently a micro-climate that facilitates recovery after disturbance such as from fire (Geldenhuys 1980). Disturbances in Afrotropical forest are usually in the form of canopy gaps and are important for maintaining species diversity and successional dynamics (Geldenhuys 1982). Typical natural gap-forming disturbances in Afrotropical forest can be small, for example caused by wind-fall, senescence, or lightning strikes of individual trees (Geldenhuys 1982), or larger, for example due to fires (Geldenhuys 1994; Giddey et al. 2021). Forest regrowth in larger fire-created gaps tends to be slower compared to regrowth after smaller gap-forming disturbances (Ella 2005; Moolman and Rikhotso 2010a), and is likely due to an altered micro-climate (Everard 1986). Furthermore, fire may create large gaps that are exposed and susceptible to invasion by alien plants such as *Acacia* (Moolman and Rikhotso 2010b), *Pinus*, *Eucalyptus*, and *Populus* species (Geldenhuys et al. 2017).

The post-fire survival of trees has been investigated in the context of tropical forests (Woods 1989; van Nieuwstadt and Sheil 2005; Hoffmann et al. 2009; Brando et al. 2012, 2014) and temperate forests (Catry et al. 2010; Shafiei et al. 2010; Wang et al. 2012; Fairman et al. 2019) but the effect of fire severity, in particular, on post-fire tree survival has only been considered in the temperate eucalypt forests of Australia (Knox and Clarke 2011; Bennett et al. 2016; Etchells et al. 2020). Fire severity is the immediate effect or damage that fire has on an ecosystem due to fire intensity, fuel consumption (e.g., biomass consumption or charring), and fire residency time (Michaletz and Johnson 2007; Keeley 2009). In the southern Cape of South Africa, extensive tracts of fynbos shrublands that abut Afrotropical forest have been converted to pine (*Pinus*) plantations, which has been shown to disrupt the natural patterns of fire spread and severity in the landscape (Kraaij et al. 2011, 2018; Giddey et al. 2021). When the natural forest-fynbos ecotone is altered, for instance through the transformation of fynbos to pine plantations, Afrotropical forest may experience unnatural variation in fire severity (Giddey et al. 2021). In turn, fire severity may affect the survival rate of forest trees (Michaletz and Johnson 2007), although in some cases this effect may be minimal, e.g., in sclerophyll forest of eastern Australia (Knox and Clarke 2011) and in dune thicket in the southern Cape of South Africa (Strydom et al. 2020). The effect of fire severity on the survival of Afrotropical forest canopy species remains largely unknown (Dargavel

2006) but requires investigation in light of altered fire regimes in the southern Cape (Kraaij et al. 2018; Giddey et al. 2021).

Traits that may influence a tree's ability to survive fire include bark thickness and stem diameter (Michaletz and Johnson 2007; Hoffmann et al. 2009; Brando et al. 2012). However, the mechanisms by which these traits affect fire-induced tree mortality are multifaceted and largely unknown (Brando et al. 2012). Bark is a good insulator as its thermal diffusivity is poor and thicker bark increases the protection of a tree's cambium from fire (Hoffmann and Franco 2003; Michaletz and Johnson 2007; Brando et al. 2012). For example, hardwood trees of the southern Amazon basin with a bark thickness of  $\geq 17$  mm are deemed fire resistant (survival probability of  $\geq 75\%$ ), while trees with a bark thickness  $\leq 5$  mm are fire sensitive (survival probability of  $\leq 25\%$ ) (Brando et al. 2012). The relationship between bark thickness and stem diameter (or relative bark thickness) may provide insight into the historical fire regime that a vegetation type has adapted to, with relative bark thickness and a species' ability to survive fire being related to the extent of fire exposure (Lawes et al. 2013; Hempson et al. 2014). For example, in Australia, fire prone tropical savanna trees had a thicker bark relative to stem diameter compared to that in non-fire prone forest trees (Lawes et al. 2013). Similarly, thick sapling bark is typical of trees in habitats with open canopies (e.g., savanna systems) associated with frequent low intensity fires thus increasing survival probability from an early developmental stage (Jackson et al. 1999). Conversely, thin sapling bark is common in trees in closed-canopy forest experiencing low frequency and low intensity fires and subsequently thick bark development is deferred until the tree is mature (Jackson et al. 1999).

Afrotropical forest predominantly experiences low intensity fire (Giddey et al. 2022) and fires are very infrequent (centuries apart, Archibald et al. 2010). This may explain the positive linear relationship between bark thickness and stem diameter generally exhibited by Afrotropical tree species (van Laar and Geldenhuys 1975) as fire is not a consistent threat and, therefore, resources are not allocated to early bark development. The relationship between bark thickness and stem diameter (van Laar and Geldenhuys 1975; Hoffmann and Franco 2003) and the dependence of bark thermal diffusivity on bark thickness (Michaletz and Johnson 2007) suggest that stem diameter is a basic and highly relevant predictor of post-fire survival in Afrotropical forest trees. Accordingly, in a single patch of burnt Afrotropical forest in the southern Cape, small trees ( $< 20$  cm diameter at breast height) incurred 68% mortality while large trees ( $> 20$  cm diameter at breast height) incurred 6% mortality (Watson and Cameron 2001). Trees with

larger stem diameter also showed higher survival rates in tropical forest in the Amazon (Brando et al. 2012), temperate broadleaved mixed forest in China (Wang et al. 2012), and temperate eucalypt forest in Australia (Fairman et al. 2019). However, this is not true for all species. Southern Cape dune thicket shares numerous species with Afrotropical forest and some species, for example *Sideroxylon inerme* (taxonomic authorities and common names of species are provided in Table 1) showed reduced survival post-fire in larger individuals than in smaller individuals (Strydom et al. 2020).

Tree architecture, i.e., tree height and stem count, furthermore affects flammability (Archibald and Bond 2003) and thus a tree's ability to survive after fire (Hoffmann et al. 2009; Burger and Bond 2015). Trees may resprout from the base, stem, and/or canopy (Kauffman 1991). The advantage of persistence through disturbance that is conferred by resprouting (Lawes and Clarke 2011) is, however, traded-off with energy allocated to storage rather than to vertical growth and seed production (Chapin et al. 1990; Kruger et al. 1997). Resprouting may be a disadvantage for canopy species in taller forests which require fast vertical growth in competition for light (Kruger et al. 1997; Archibald and Bond 2003) or to escape the "fire trap" (Hoffmann et al. 2009). For example, tall forests are generally dominated by reseeders, while short forests are dominated by resprouters (Kruger et al. 1997). It is therefore conceivable that fire-avoiding Afrotropical forest trees may not allocate energy to storage reserves, particularly in tall mature stands. Consequently, these species may not be able to resprout, even if they are capable of resprouting in short vegetation types that experience more regular disturbance (Strydom et al. 2021). The role that resprouting plays in the recovery of Afrotropical forest has received little attention (Kruger et al. 1997; Bond and Midgley 2001) and comprehensive information on the responses to fire of Afrotropical forest tree species does not exist in the primary literature (Lawes et al. 2004).

An extensive wildfire (70 000 ha) in the southern Cape of South Africa between the towns of George and Knysna during October–November 2018 (hereafter the 2018 George fire) burnt 4628 ha of Afrotropical forest (Giddey et al. 2022) providing an ideal opportunity to explore the resilience of Afrotropical forest trees to fire. In particular, we assessed the effect of fire severity and tree size on the post-fire survival of a comprehensive set of Afrotropical forest tree species.

## Methods

### Study area

Afrotropical forest occurs within the Cape Floristic Region of South Africa at 34.0° S and between 22.0° E and

24.3° E. Mean winter temperatures are mild with a minimum of 7°C and maximum of 19°C in June, while mean summer temperatures are moderately warm with a minimum of 22°C and maximum of 25°C in January (Bond 1981). The region experiences precipitation all year round with mean annual rainfall between 800 mm and 1100 mm (Tyson and Preston-Whyte 2000). Afrotropical forest occurs on nutrient-poor sandstone-derived soils typical of the region (van Daalen 1984).

There are 47 canopy and 40 subcanopy tree species in Afrotropical forest, including various emergent species (Geldenhuys 1989), and 14 of these species are dominant (Seydack et al. 2012). The two most common canopy species in Afrotropical forest are *Olea capensis macrocarpa* and *Podocarpus latifolius* (Seydack et al. 2012). Afrotropical forest can be further classified into coastal, plateau, and mountain forest types based on their disturbance regime and resulting species composition (Mucina and Geldenhuys 2006). Mountain forest generally experiences more severe and frequent fires compared to coastal and plateau forest (Geldenhuys 1994). As a result, canopy species of mountain forest largely include those which are assumed to be well adapted to disturbance, e.g., *Ocotea bullata* and *Cunonia capensis*, and these forests are less diverse than coastal and plateau forest (Geldenhuys 1989).

Fire in the study region may occur at any time of the year with fire danger weather peaking in the dry summer months and in autumn and winter when warm and dry katabatic or "berg" winds are common (Kraaij et al. 2013a, b). The 2018 George fire burnt from 31st of October to the 6th of November (Giddey et al. 2021). The fire occurred during high fire danger weather conditions similar to those experienced during the extreme June 2017 fire in the region and an extended drought that preceded both these fires (Kraaij et al. 2018). We focused on the largest contiguous portion of the 2018 George fire scar between the towns of George in the west and Knysna in the east (Fig. 1), which largely occurred within the confines of the Garden Route National Park. A total of 4 628 ha of Afrotropical forest burnt with over 1 500 ha burnt at a medium to high severity (Giddey et al. 2022).

### Fire severity, tree size, and survival

Within the areas of forest that burnt in the 2018 George fire, we demarcated survey plots of 20 m × 20 m in mountain and plateau forest. We used a stratified random sampling design to ensure survey effort across the range of fire severities (estimated from the differenced Normalised Burn Ratio calculated per 20 m × 20 m pixel; Giddey et al. 2022) experienced by these forests (Fig. 1). We measured tree size in terms of diameter at

**Table 1** Percentage of individuals that survived post-fire, percentage of individuals resprouting from the stem, mean tree size, and sample number of Afrotemperate forest species surveyed. Species are listed in descending order of percentage survival, and species with sample size of  $\geq 20$  are indicated in bold text. Nomenclature follows [www.theplantlist.org](http://www.theplantlist.org)

Species	Common name	% Survival	% Resprouting from stem	Mean tree stem diameter (cm)	Sample number
<i>Cunonia capensis</i> L.	Red alder	100	50	35	2
<i>Diospyros dichrophylla</i> (Gand.) De Winter	Star apple	100	100	18	5
<i>Gymnosporia buxifolia</i> (L.) Szyszyl.	Spike thorn	100	100	11	2
<i>Ilex mitis</i> (L.) Radlk.	Cape holly	100	67	54	3
<i>Prunus africana</i> (Hook.f.) Kalkman	Red stinkwood	100	100	25	2
<i>Scolopia mundii</i> Warb.	Red pear	100	100	16	2
<i>Scolopia zeyheri</i> (Nees) Szyszyl.	Thorn pear	100	100	25	1
<i>Scutia myrtina</i> (Burm.f.) Kurz	Cat thorn	100	100	11	1
<i>Searsia chirindensis</i> (Baker f.) Moffett	Red currant	100	50	37	4
<i>Searsia lucida</i> (L.) F.A.Barkley	Glossy currant	100	100	15	1
<i>Sideroxylon inerme</i> L.	Milkwood	100	100	19	3
<b><i>Ocotea bullata</i> (Burch.) E. Meyerx in Drege<sup>D</sup></b>	Stinkwood	<b>85</b>	<b>72</b>	<b>35</b>	<b>48</b>
<b><i>Lachnostylis hirta</i> (L.f.) Müll.Arg.</b>	Coal wood	<b>80</b>	<b>80</b>	<b>17</b>	<b>20</b>
<i>Olea capensis</i> L.	Small ironwood	75	75	16	8
<b><i>Cassine peragua</i> L.<sup>T</sup></b>	Cape saffron	<b>71</b>	<b>62</b>	<b>19</b>	<b>21</b>
<i>Platylophus trifoliatus</i> D.Don <sup>D</sup>	White alder	71	71	50	7
<i>Acacia melanoxylon</i> R.Br. <sup>A</sup>	Black wood	67	67	26	3
<i>Diospyros whyteana</i> (Hiern) P.White	Bladder-nut	65	65	16	17
<i>Nuxia floribunda</i> Benth. <sup>D</sup>	Forest alder	63	50	41	8
<b><i>Rapanea melanophloeos</i> (L.) Mez<sup>D,T</sup></b>	Cape beach	<b>63</b>	<b>54</b>	<b>23</b>	<b>108</b>
<i>Canthium inerme</i> (L.f.) Kuntze	Turkey-berry	59	47	16	17
<i>Ekebergia capensis</i> Sparrm.	Cape ash	57	57	48	7
<b><i>Afrocarpus falcatus</i> (Thunb.) C.N.Page<sup>D</sup></b>	Outeniqua yellowwood	<b>56</b>	<b>16</b>	<b>34</b>	<b>55</b>
<b><i>Pterocelastrus tricuspidatus</i> Walp.<sup>D,T</sup></b>	Candle wood	<b>53</b>	<b>48</b>	<b>23</b>	<b>128</b>
<b><i>Apodytes dimidiata</i> E.Mey. ex Arn.<sup>D,T</sup></b>	White pear	<b>52</b>	<b>39</b>	<b>23</b>	<b>23</b>
<i>Canthium mundianum</i> Cham. & Schltdl.	Rock alder	50	0	18	2
<i>Robsonodendron eucleiforme</i> (Eckl. & Zeyh.) R.H.Archer	White silky-bark	50	25	16	4
<b><i>Curtisia dentata</i> (Burm.f.) C.A.Sm<sup>D</sup></b>	Assegai	<b>44</b>	<b>22</b>	<b>23</b>	<b>72</b>
<b><i>Gonioma kamassi</i> E.Mey.</b>	Kamassi	<b>44</b>	<b>27</b>	<b>16</b>	<b>179</b>
<b><i>Olinia ventosa</i> (L.) Cufod<sup>D</sup></b>	Hard pear	<b>44</b>	<b>31</b>	<b>43</b>	<b>120</b>
<i>Burchellia bubalina</i> (L.f.) Sims	Wild pomegranate	40	40	15	5
<b><i>Elaeodendron croceum</i> (Thunb.) DC.</b>	Saffron	<b>35</b>	<b>35</b>	<b>17</b>	<b>60</b>
<b><i>Halleria lucida</i> L.<sup>T</sup></b>	Tree fuchsia	<b>35</b>	<b>26</b>	<b>15</b>	<b>23</b>
<b><i>Podocarpus latifolius</i> (Thunb.) R.Br. ex Mirb.<sup>D</sup></b>	Real yellowwood	<b>35</b>	<b>8</b>	<b>21</b>	<b>181</b>
<b><i>Olea capensis</i> L. <i>macrocarpa</i> (C.H.Wr.) Verd.<sup>D</sup></b>	Ironwood	<b>16</b>	<b>9</b>	<b>26</b>	<b>139</b>
<i>Maytenus acuminata</i> (L.f.) Loes.	Silky bark	0	0	15	2
<i>Myroxyylon aethiopicum</i> (Thunb.) Loes.	Spoonwood	0	0	11	1
<i>Pinus pinaster</i> Aiton <sup>A</sup>	Pine	0	0	12	2
<i>Psyrax obovata</i> (Klotzsh ex Eckl. and Zeyh.) Bridson <sup>D</sup>	Quar	0	0	19	1
<i>Virgilia divaricata</i> Adamson	Blossom tree	0	0	26	12
Unknown identity		18	13	25	79
All species collectively		45	32	24	1378

<sup>D</sup> Dominant canopy species (Seydack et al. 2012)<sup>T</sup> Species common to dune thicket (Strydom et al. 2020)<sup>A</sup> Species that are alien (non-native) to the study area



**Fig. 1** The portion of the fire (outlined in white) that burnt during 31 October–6 November 2018 between the towns of George and Knysna, indicating survey plots where fire severity and tree survival were assessed. Imagery source: Google Earth image (December 2018), EPSG:3857 - WGS 84/Pseudo-Mercator – Projected

breast height (1.5 m above ground) of the main stem and estimated tree height to the nearest meter. Pre-burn bark thickness could not be measured as our surveys were done after a wildfire. Each tree with a stem diameter at breast height of > 10 cm located inside the survey plot was visually assessed for the fire severity it experienced in terms of two measures, namely (i) the char height from the ground along the main stem, estimated to the nearest meter, and (ii) the char depth rated as the damage to the bark and wood of the main stem between 0 and 2 m above ground using the methods of Giddey et al. (2022) and Strydom et al. (2020) as follows: (1) low—light charring of bark (patchy charring on the surface of the bark); (2) medium—extensive charring of bark and wood (bark blackened and charring of the wood) and/or damage to bark (bark cracking or burnt away); and (3) high—substantial damage to the wood (charcoaled or burnt away). Destroyed trees, i.e., with remaining burnt stems of less than 1.5 m above ground were assessed if the stem was > 10 cm diameter at the highest remaining point. We considered trees to have survived if they had green foliage in the canopy and/or resprouted from the base (basal resprouting) or the main stem (epicormic resprouting) (Wigley et al. 2020). We did not consider axillary resprouting in the canopy as it was difficult to discern pre-fire growth from post-fire resprouting in many species. We undertook all surveys between the end of May 2020 and the beginning of November 2020, i.e., 19 to 24 months post-fire and a total of 88 plots, 40 species and 1 378 trees were surveyed (Table 1).

#### Data analysis

We assessed the survival response of Afrotropical forest trees from all study species collectively with a mixed

effects logistic regression model (binomial family, logit link function) using the *lme4* package (Bates 2010) in the open-source R software version 4.0.2 (R Development Core Team, 2019). To test for collinearity among factors, we used Spearman-rank correlation and regarded  $r_s = 0.6$  as a threshold for inclusion of both factors into a model (Tabachnick and Fidell 1996). Our two measures of fire severity, i.e., char height and char depth, were collinear ( $r_s = 0.67$ ,  $p < 0.05$ ), and we retained char depth as the preferred proxy of fire severity. Our two measures of tree size, i.e., stem diameter and tree height, were also collinear ( $r_s = 0.71$ ,  $p < 0.05$ ), and we retained stem diameter as the preferred measure of tree size. We also tested for collinearity between fire severity and tree size, but this relationship was weak ( $r_s = 0.05$ ,  $p < 0.05$ ), and both factors were retained. As predictors of survival, we thus included fire severity, tree size, and their interaction as fixed factors, while species were included as a random factor. Fire severity was treated as a three-level ordered factor (Strydom et al. 2020). There was no significant interaction between fire severity and tree size ( $\text{Chsq} = 5.098$ ,  $p > 0.05$ ), and therefore, the interaction was excluded from the final model. We likewise used logistic regression models (binomial family, logit link function) to assess the survival response of individual species with a sample number > 40 (Table 1), in relation to fire severity and tree size. For all models, we used a Type II Wald chi-square test (Hastie and Pregibon 1992) to compute the significance of fixed factors and the *MuMIn* package (Barton 2009) to calculate conditional and marginal  $R^2$  values.

#### Results

The post-fire survival rate of all trees collectively ( $n = 1\,378$ ) was 45% (Table 1). The results of the logistic regression for survival of all trees collectively showed that

fire severity had a significant negative effect on survival while tree size had a significant positive effect on survival (Fig. 2; Table 2). The total variance explained by the model was 40.8%; the fixed factors combined explained 13.2% of this variance, and species as a random factor explained 27.6%.

Respective tree species showed differential post-fire survival responses to fire (Table 1). Species (with a sample no.  $\geq 20$ ) showing a high survival rate ( $>60\%$ ) were *Ocotea bullata*, *Lachnostylis hirta*, *Cassine peragua*, and *Rapanea melanophloeos*, while species showing low survival ( $<40\%$ ) were *Olea capensis macrocarpa*, *Podocarpus latifolius*, *Elaeodendron croceum*, and *Halleria lucida*. Most species surveyed (and 32% of all individual trees surveyed) were capable of resprouting from the stem. The exceptions were *Canthium mundianum*, *Maytenus acuminata*, *Mystroxyloa aethiopicum*, *Psyrdrax obovata*, *Virgilia divaricata*, and *Pinus pinaster*, although for these exceptions (bar *Virgilia divaricata*), the sample size was small ( $<2$  individuals). Dominant canopy species which showed strong resprouting from the stem ( $>70\%$  of individuals resprouted) were *Ocotea bullata* and *Lachnostylis hirta*, whereas those showing poor resprouting from the stem ( $<20\%$  of individuals resprouted) were *Podocarpus latifolius*, *Olea capensis macrocarpa*, and *Afrocarpus falcatus*.

A total of 10 species (with sample number  $>40$ ; Table 1), of which 8 were dominant canopy species

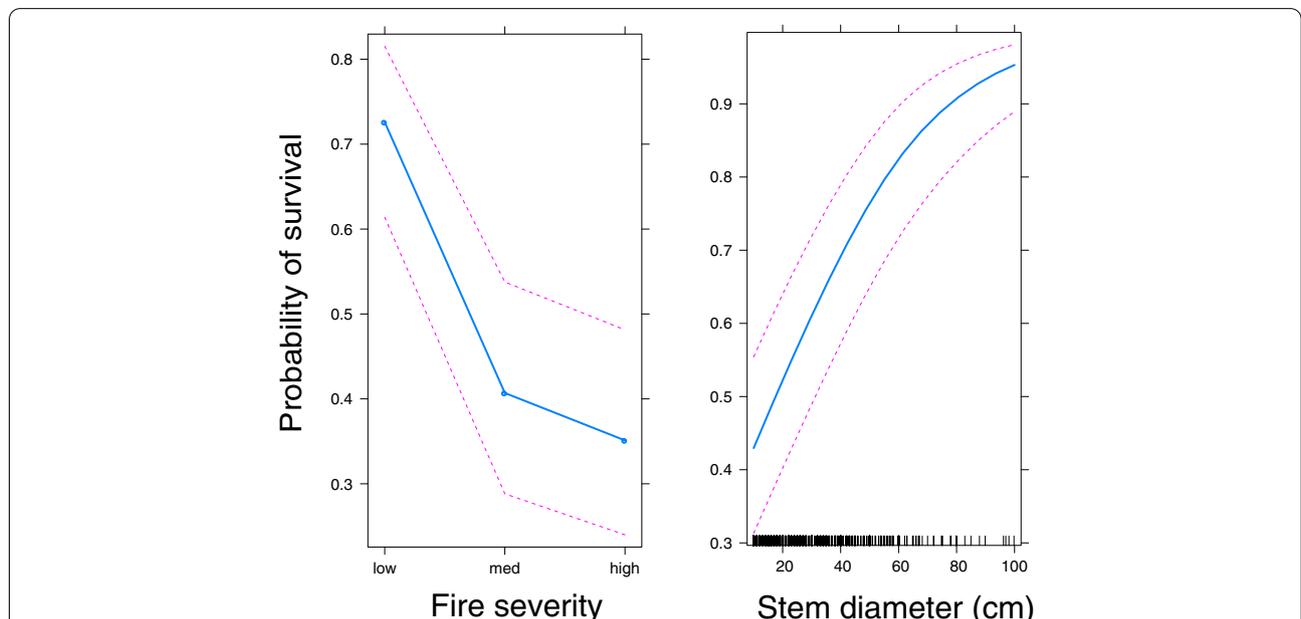
**Table 2** Output of logistic regression model (binomial family, logit link function) investigating the effects of tree size and fire severity on post-fire Afrotemperate forest tree survival. Fixed factors were tree size and fire severity (L, linear; Q, quadratic), and species was a random factor

Survival	Estimate	Chisq <sup>a</sup>
Fire severity	- 1.123 (L) 0,454 (Q)	$< 2.2e^{-16***}$
Tree size	0.036	$1.878e^{-12***}$

Significance: \*\*\* $p < 0.001$

<sup>a</sup> Chisq statistics and significance levels were obtained from deviance tables (Type II Wald chi-square tests)

(Seydack et al. 2012), were individually investigated for the effect of fire severity and tree size on survival. Fire severity and tree size had no significant effect on the survival of *Curtisia dentata* and *Elaeodendron croceum* (Fig. 3; Table 3). Fire severity had a significant negative effect on the survival of *Afrocarpus falcatus*, *Gonioma kamassi*, *Olea capensis macrocarpa*, *Pterocelastrus tricuspidatus*, *Podocarpus latifolius*, *Olinia ventosa*, and *Ocotea bullata*, while tree size had a significant positive effect on the survival of *Rapanea melanophloeos*, *Ocotea bullata*, *Olinia ventosa*, and *Podocarpus latifolius*. The species with the highest variance explained by the models were *Ocotea bullata* ( $R^2=0.95$ ) and *Olea capensis macrocarpa* ( $R^2=0.91$ ). *Ocotea bullata* showed a 100% survival probability to low and medium fire severity, but



**Fig. 2** Predicted probability of survival 19–24 months post-fire of Afrotemperate forest canopy trees in relation to fire severity and stem diameter. Fire severity was observed on the stem between 0 and 2 m above ground and rated: low fire severity—light charring of bark; medium fire severity—extensive charring of bark and some damage to wood; and high fire severity—extensive damage to the wood. Tree size was measured in terms of diameter at breast height (1.5 m above ground)

survival was reduced to 50% when exposed to high fire severity. Large *Ocotea bullata* trees (stem diameter of > 30 cm) survived more frequently than smaller individuals. *Olea capensis macrocarpa* showed low survival probability (< 20%) across all fire severity classes and showed no significant increase in survival with tree size.

## Discussion

Our study presents the first comprehensive assessment of post-fire Afrotemperate forest tree species survival after a large wildfire. The average survival rate across all individuals from a mix of species representative of the composition of mountain and plateau forest was 45%. Relative to documented tree survival rates 8–60 months post-fire in other forests of the world, Afrotemperate forest is most comparable to coniferous forest in North America (50% survival; Hood et al. 2007), tropical forest bordering savanna in Brazil (48%; Hoffmann et al. 2009), and tropical forest in Malaysia (43%; Woods 1989), but higher than that in tropical forest in Indonesia (26%; van Nieuwstadt and Sheil 2005) and notably lower than that in temperate karri forest in western Australia (74%; Etchells et al. 2020), neighboring dune thicket in South Africa (83%; Strydom et al. 2020), and temperate mixed forest in Portugal (92%; Catry et al. 2010). The differing post-fire survival rates among forest types may be a consequence of the historical fire regimes that these forests have adapted to, with species' ability to survive fire being related to the extent of fire exposure (Hoffmann et al. 2009; Lawes et al. 2013). However, the effect of fire regimes on fire survival traits within vegetation types requires further investigation.

In our study, the average post-fire survival rate of small trees (< 20 cm stem diameter) was approximately 50% lower than that of large trees (> 80 cm stem diameter) (Fig. 2). On average, trees became fire resilient ( $\geq 75\%$  survival probability) at 50 cm stem diameter. Based on the time taken for a tree to grow to a size that would be fire resilient, the fire return interval that will maintain forest can be estimated. Considering that the mean annual diameter increment per annum for eight common Afrotemperate canopy species is 0.19 cm (SAN-Parks 2019), it will take approximately 210 years for a 10 cm diameter tree to reach 50 cm in diameter. Therefore, Afrotemperate forest composition and structure will probably not be maintained if high intensity fires occur at intervals of less than 200 years, and forest patches will

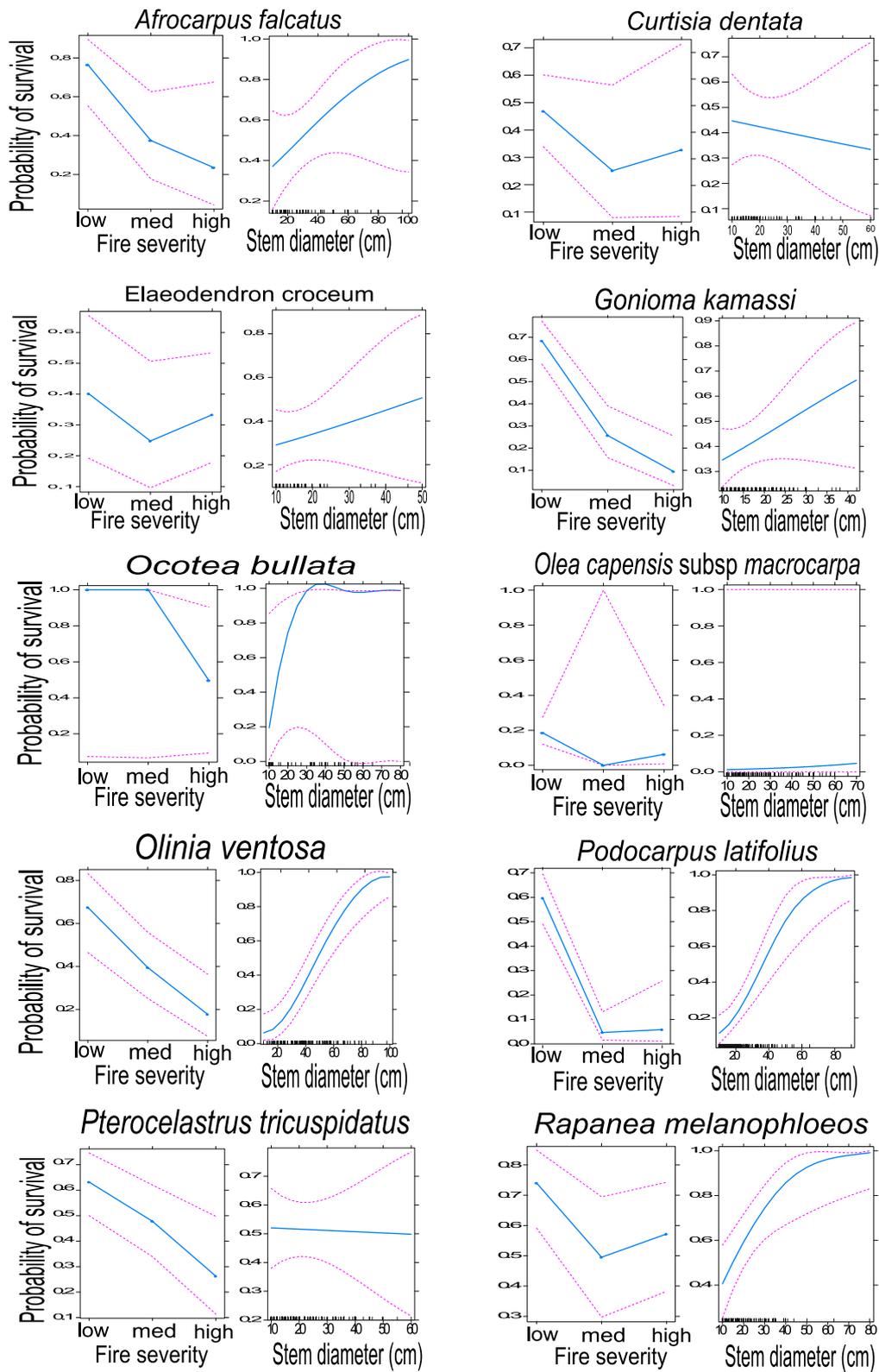
likely transition to fynbos at fire intervals of less than 50 years (van Wilgen et al. 1990; Kraaij and van Wilgen 2014). However, this is a very crude prediction as there are numerous variables affecting tree growth rates even within species. For example, the time taken for a sapling to reach 10 cm diameter has not been considered as these data are not available (G. Durrheim in litt. 2022/02/07) and is presumably variable due to factors such as light, nutrient, and water availability (cf. Hoffmann et al. 2012). Furthermore, existing data on tree growth rates are from unburnt forests, whereas regrowth in burnt forest tends to be slower than growth in intact forest and regrowth after smaller gap-forming disturbances (Ella 2005; Moolman and Rikhotso 2010a).

Our results further showed that post-fire tree survival was negatively related to our proxy measure of fire severity, and this effect in Afrotemperate forest was more pronounced than that observed in the adjacent dune thicket (Strydom et al. 2020). At the level of individual species, those species common to both vegetation types (Table 1) on average showed a 29% lower post-fire survival rate in Afrotemperate forest than in dune thicket. Fires are infrequent in forest transitions in South Africa, and although there are no reliable records, estimates from remote sensing suggest that fires are centuries apart (Archibald et al. 2010), compared to around 50 years in dune thicket (Cowling et al. 1997; Cowling and Potts 2015). This comparison thus further supports the notion of improved fire resilience in species or vegetation types that are more exposed to frequent or severe fires, as is also seen in comparisons between savanna and forest (Hoffmann and Franco 2003; Lawes et al. 2013). Therefore, fire may also drive intraspecific functional traits of trees that ensure resilience depending on the frequency and severity of fire experienced by a vegetation type.

All Afrotemperate forest tree species for which we surveyed sufficient numbers of individuals exhibited an ability to resprout from the stem. This finding is in contrast with previous assertions that several common canopy species, including *Podocarpus latifolius*, *Afrocarpus falcatus*, *Scutia myrtina*, *Scolopia mundii*, and *Rapanea melanophloeos*, are unable to resprout and often die when above ground parts are destroyed (Geldenhuys 1989, 1994; van Daalen 1993; Vermeulen 1995). Thirty-two percent of trees surveyed, irrespective of species, resprouted from the stem. Considering that survival of all trees collectively was 45%, it appears that resprouting from the

(See figure on next page.)

**Fig. 3** Predicted probability of post-fire survival (note disparate scaling of y-axes) of Afrotemperate forest tree species in relation to fire severity and tree size (in columns). Fire severity was observed on the main stem between 0 and 2 m above ground and rated: low fire severity—light charring of bark; medium fire severity—extensive charring of bark and some damage to wood; and high fire severity—extensive damage to the wood. Tree size was measured in terms of stem diameter at breast height (1.5 m above ground)



**Fig. 3** (See legend on previous page.)

**Table 3** Output of logistic regression models (binomial family, logit link function) investigating species-specific survival response in relation to fire severity and tree size. Effects include fire severity and tree size (L, linear; Q, quadratic)

Species	Fire severity		Tree size		Model $R^{2b}$
	Estimate	Chisq <sup>a</sup>	Estimate	Chisq <sup>a</sup>	
<i>Afrocarpus falcatus</i>	− 1.666 (L) 0.417 (Q)	8.680*	0.030	2.173	0.203
<i>Curtisia dentata</i>	− 0.429 (L) 0.556 (Q)	1.994	− 0.003	0.015	0.047
<i>Elaeodendron croceum</i>	− 0.208 (L) 0.459 (Q)	0.840	0.022	0.564	0.038
<i>Gonioma kamassi</i>	− 2.140 (L) 0.255 (Q)	47.079***	0.041	2.129	0.316
<i>Ocotea bullata</i>	− 8.213 (L) − 3.199 (Q)	16.538***	0.425	14.509***	0.953
<i>Olea capensis macrocarpa</i>	− 0.864 (L) 13.347 (Q)	7.776*	0.023	2.109	0.916
<i>Olinia ventosa</i>	− 1.600 (L) 0.019 (Q)	13.239**	0.070	28.355***	0.438
<i>Podocarpus latifolius</i>	− 2.183 (L) 1.117 (Q)	53.738***	0.043	11.563***	0.412
<i>Pterocelastrus tricuspidatus</i>	− 1.112 (L) − 0.129 (Q)	8.376*	− 0.001	0.010	0.084
<i>Rapanea melanophloeos</i>	− 0.535 (L) 0.561 (Q)	4.640	0.072	9.714**	0.210

Significance codes: \* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.001$

<sup>a</sup> Chisq statistics and significance levels were obtained from deviance tables (Type II Wald chi-square tests)

<sup>b</sup>  $R^2$  values were derived using the  $R^2$  GLMM function in the *MuMIn* package

stem is a primary means of post-fire recovery in Afrotropical forest trees. Furthermore, axillary resprouting was not recorded; however, many trees seemed to have been resprouting from the canopy. Therefore, further investigation of the axillary resprouting of Afrotropical forest is required and may reveal that resprouting has an even greater role in post-fire recovery of Afrotropical forest. Species with a strong resprouting ability (e.g., *Ocotea bullata* and *Lachnostylis hirta*) may act as nurse species and may facilitate post-fire germination of shade tolerant species with poor resprouting ability such as *Olea capensis macrocarpa* and *Podocarpus latifolius*. These results provide promising evidence for the conservation of canopy species which are predominantly reseeders and were previously assumed unable to persist through large disturbances (Kruger et al. 1997). When comparing the incidence of resprouting from the stem in co-occurring species between taller stature Afrotropical forest and shorter stature dune thicket, it seems notably higher in dune thicket. Five species investigated in our study (with sample no. > 20) co-occur in dune thicket (Table 1) and showed lower incidence of resprouting in Afrotropical forest (46% of individuals) than in dune thicket (87%; Strydom et al. 2020). Therefore, the investment of resources in resprouting may be less in canopy species of tall forests which require fast vertical growth in

competition for light than in a shorter stature forest and thicket (Kruger et al. 1997; Chapin et al. 1990; Archibald and Bond 2003; Strydom et al. 2021).

Bark thickness is a trait that may have enhanced fire tolerance in certain species. For example, both *Ocotea bullata* and *Rapanea melanophloeos* have thick bark (Philips 1927; van Laar and Geldenhuys 1975) which may have contributed to their high survival rates observed in this study. However, species such as *Olea capensis macrocarpa* and *Curtisia dentata* are also considered to have thick bark yet they showed lower survival rates than some species with thin bark such as *Afrocarpus falcatus* and *Olinia ventosa* (Philips 1927; van Laar and Geldenhuys 1975). Therefore, there may be other factors that influence a tree's ability to survive fire such as wood density and root depth (Granger 1984). A positive relation between wood density and post-fire survival has been shown in hardwood trees of the Amazon; therefore, wood density may be an important factor in determining a tree's ability to survive fire (Brando et al. 2012). Deeper roots will be less affected by smouldering surface fire; therefore, root depth may be important for patches of Afrotropical forest where fire is present for an extended length of time (Granger 1984). In Afrotropical forest, a root depth of  $\geq 0.6$  m is assumed adequate for protection against surface fire (Philips 1927);

however, little is known about the average root depth of Afrotropical forest species. The root to shoot ratio of trees may also be important as it represents their below-ground carbohydrate reserves and thus their ability to resprout after fire (Hoffmann and Franco 2003).

Globally fire is an important driver of species diversity (Pausas and Ribeiro 2017). For example, species composition and diversity of Afrotropical forest patches have in part been linked to the frequency and severity of fire along gradients (Geldenhuys 1994). Afrotropical forest margins and mountain forest typically experience more frequent and severe fires and are less diverse than the forest core and plateau forests which are less fire-prone (Geldenhuys 1994; Watson and Cameron 2001). In our study, Afrotropical forest trees showed a divergent survival response to fire. Species showing the highest survival (> 60%) were *Ocotea bullata*, *Lachnostylis hirta*, *Cassine peragua*, and *Rapanea melanophloeos*. Species showing lowest survival (< 40%) were *Elaeodendron croceum*, *Halleria lucida*, *Podocarpus latifolius*, and *Olea capensis macrocarpa*. Species with high survival rates can be deemed fire tolerant and will likely dominate forest margins and mountain forest, while species with low survival rates are less fire tolerant and will likely be restricted to forest core and plateau forest. For example, *Podocarpus latifolius* and *Olea capensis macrocarpa* had the lowest survival rates post-fire and are slow growing and shade tolerant (van Daalen 1991). However, they are dominant canopy species and undergo mast seeding events resulting in good regeneration in intact forest (Geldenhuys 1989). On the contrary, fire tolerant species that are strong resprouters (e.g., *Ocotea bullata*, *Cunonia capensis* and *Rapanea melanophloeos*) are likely to dominate more fire-exposed mountain forest, while some species may occur in a range of forest types experiencing different levels of fire exposure (e.g., *Pterocelastrus tricuspidatus* and *Sideroxylon inerme*) due to their plasticity of reproductive and growth characteristics (Kruger et al. 1997). Therefore, species diversity and richness depend on the persistence of mountain and plateau forest, and their associated disturbance regimes. This study showed that in some species (e.g., *Podocarpus latifolius* and *Olinia ventosa*) small (< 30 cm) individuals suffer high post-fire mortality and these species would therefore be particularly vulnerable to frequent fires. Furthermore, *Afrocarpus falcatus*, *Gonioma kamassi*, *Ocotea bullata*, *Olea capensis macrocarpa*, *Olinia ventosa*, *Pterocelastrus tricuspidatus*, and *Podocarpus latifolius* are sensitive to high severity fire. Therefore, frequent and high severity fires may reduce these species' populations and ultimately alter forest species composition and diversity. Potential future changes in fire regimes due to

climate change (Kraaij et al. 2013a), increased sources of ignition (Kraaij et al. 2013b), habitat fragmentation, and alien tree plantations and invasions (Kraaij et al. 2011; Giddey et al. 2021) are thus likely to result in changes to the composition of forests, with consequences for their conservation.

## Conclusion

Fire severity and tree size are significant determinants of post-fire survival of Afrotropical forest trees and species vary in their tolerance to fire. Furthermore, the survival response and resprouting abilities of Afrotropical forest and neighboring, more fire-exposed dune thicket differ, suggesting that the historical fire regimes associated with vegetation types likely drive species adaptations. Our findings suggest that fire severity and fire frequency (in terms of how tree size relates to fire frequency) are important for maintaining species richness and diversity within and between forest types. This implies that potential changes in fire regimes due to global change will have consequences for the conservation of forests.

## Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s42408-022-00128-5>.

Additional file 1.

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## Authors' contributions

All authors participated in the conceptualization and design of the study; BG undertook the field data collection and most of the data analyses; all authors participated in the writing of the manuscript. The author(s) read and approved the final manuscript.

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## Availability of data and materials

Data will be uploaded in spreadsheet format as a [supplementary](#).

## Declarations

### Ethics approval and consent to participate

Our study involved non-destructive observations of plants and thus did not require ethics approval. We have obtained permission from the government authority on whose land we undertook field surveys (South African National Parks permit Ref. KRAA-T/2019-010) and their approval is *inter alia* subject to adherence to all local, national, or international guidelines and legislation relevant to research of this nature.

**Consent for publication**

Not applicable.

**Competing interests**

The authors declare that they have no competing interests.

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