Forest Ecosystems

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A combination of climate, tree diversity and local human disturbance determine the stability of dry Afromontane forests

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Abstract

Background: Anthropogenic disturbances are increasingly affecting the vitality of tropical dry forests. The future condition of this important biome will depend on its capability to resist and recover from these disturbances. So far, the temporal stability of dryland forests is rarely studied, even though identifying the important factors associated with the stability of the dryland forests could serve as a basis for forest management and restoration.

Methodology: In a degraded dry Afromontane forest in northern Ethiopia, we explored remote sensing derived indicators of forest stability, using MODIS satellite derived NDVI time series from 2001 to 2018. Resilience and resistance were measured using the anomalies (remainders) after time series decomposition into seasonality, trend and remainder components. Growth stability was calculated using the integral of the undecomposed NDVI data. These NDVI derived stability indicators were then related to environmental factors of climate, topography, soil, tree species diversity, and local human disturbance, obtained from a systematic grid of field inventory plots, using boosted regression trees in R.

Results: Resilience and resistance were adequately predicted by these factors with an R^2 of 0.67 and 0.48, respectively, but the model for growth stability was weaker. Precipitation of the wettest month, distance from settlements and slope were the most important factors associated with resilience, explaining 51% of the effect. Altitude, temperature seasonality and humus accumulation were the significant factors associated with the resistance of the forest, explaining 61% of the overall effect. A positive effect of tree diversity on resilience was also important, except that the impact of species evenness declined above a threshold value of 0.70, indicating that perfect evenness reduced the resilience of the forest. Precipitation of the wettest month was the most important factor explaining 43.52% of the growth stability variation.

Conclusion: A combination of climate, topographic factors and local human disturbance controlled the stability of the dry forest. Also tree diversity is an important stability component that should be considered in the management and restoration programs of such degraded forests. If local disturbances are alleviated the recovery time of dryland forests could be shortened, which is vital to maintain the ecosystem services these forests provide to local communities and global climate change.

Keywords: Climate, Dryland, Disturbance, Restoration, Tigray, Growth stability, Biodiversity function

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Introduction

A significant area of the globe (41%) is covered with drylands, and a large part of the human population (35%) resides in them (Safriel and Adeel 2008). Among dryland ecosystems, the dry forest biome covers an estimated 1079 million ha (Bastin et al. 2017), accounting for almost half of the (sub) tropical forests (Aide et al. 2013). Dryland forests are very important for biodiversity conservation, as they are known for their high level of endemism (Myers et al. 2000); also for deep aquifer recharge as they show high infiltration rates in a lacking water environment (Bargués-Tobella et al. 2020), and for moderating high temperatures. Dryland forests are some of the most threatened by human degradation and therefore, maintaining the remnant forests is crucial for a sustainable environment, and a seed source for possible restoration (Safriel et al. 2005; Díaz et al. 2018).

Dry forests are among the most threatened ecosystems (Bognounou et al. 2010) as they are found in regions of low productivity, supporting population with one of the fastest birth rates, where poverty prevails (Safriel and Adeel 2008). Dry forests have high conversion rates to other land use, and the remaining parts are degraded and fragmented (Sánchez-Azofeifa et al. 2005).

Due to climate change and other anthropogenic causes, desertification is widespread in drylands and is impacting the overall well-being of dwellers (Yan et al. 2011). Climate change-induced prolonged dryness could change the vegetation composition of dryland forests, which might further complicate the socioeconomic situation in these areas (Huang et al. 2016). Local disturbance factors such as illegal logging, uncontrolled browsing and grazing, and fire incidences are adding on to, and are possibly interfering with, the effect of global climate change on dryland forests (Lloret et al. 2007; Jacob et al. 2014; Abrha and Adhana 2019; Hishe et al. 2020). Understanding how forests respond to increasing climate change and local human pressure is crucial to keep a sustained flow of the ecosystem services, ecosystem stability (Jactel et al. 2006; Bauhus et al. 2017; Duffy et al. 2017) and should be an essential component of forest management (Huang et al. 2016). This is important as not all forests respond in the same way to global and local disturbances. Their responses are modulated by local landscape characteristics such as species composition, altitude, slope and edaphic factors. Diverse versus monoculture stands, for example, are reported to respond differently to disturbance (Johnson et al. 1996; Van Ruijven and Berendse 2007; De Keersmaecker et al. 2018). While a number of studies reported that tree diversity has a positive effect on production, health and stability of forests, other have reported either neutral or negative effect of diversity which indicates for a need of further study (Waide et al. 1999; McCann 2000). As a consequence restoration planning protocols will need context specific information.

Different metrics have been proposed to define and quantify the responses of forests to disturbances (Webb 2007; Yan et al. 2011). Among these, growth stability, resilience and resistance have been used widely (Verbesselt et al. 2016; De Keersmaecker et al. 2018). Many definitions are given to the mentioned stability concepts (Nikinmaa et al. 2020). The resilience is defined as the recovery rate after a disturbance (Dakos et al. 2012). Resistance, on the other hand, is the capacity of the forest to remain unchanged regardless of disturbances (Grimm and Wissel 1997). Growth stability is considered as a steady continuity of growth irrespective of external disturbance (Chen et al. 2019).

Ecosystem stability is affected by different factors, such as climate, topography and species diversity, among others (Yan et al. 2011; Hutchison et al. 2018). Insight in the response of the ecosystem to change in these factors is valuable for management and restoration purposes. In the absence of long-term ecological experiments, remote sensing data analysis is providing an opportunity to monitor long term forest dynamics (Wang et al. 2004). Typically, vegetation indices based on the ratio between the reflectance in red and near-infrared (NIR) bands, such as the Normalized Different Vegetation Index (NDVI) (Kogan 1995), are used to characterize vegetation properties (Lu et al. 2016). NDVI time series thus provide valuable information on forest dynamics and their response to external pressures (Lhermitte et al. 2011; Verbesselt et al. 2016; De Keersmaecker et al. 2018).

Forest stability metrics can be derived by applying statistical analysis to the entire NDVI time series, holistic approach, to take the possible recurrent stochastic perturbation events such as drought and other environmental variations in an open environment into consideration (Verbesselt et al. 2016; Hutchison et al. 2018). Within the holistic approach, temporal autocorrelation (TAC) (Verbesselt et al. 2016), the depth of the anomalies (De Keersmaecker et al. 2014) and the standard deviation of the anomalies (Pimm 1984) from a decomposed time series are commonly used as an indicator of forest resilience and resistance, respectively. TAC is based on the assumption that forests with lower resilience will recover more slowly, and growth progress is dependent on previous performances (Verbesselt et al. 2016). Hence, higher TAC values indicate a slow forest response to these perturbations, showing lower recovery rate of the system. TAC is thus a measure of the slowness of forest response after disturbances and a direct indicator of resilience (Verbesselt et al. 2016). TAC can be used to assess how close a system is close to a critical transition point (CTP) to another stable system, the higher the

autocorrelation (close to one) the closer the system is to the CTP (Leemput et al. 2018). Subtracting the TAC from one, on the other hand, indicates how close a system is to its prior disturbance state (the recovery rate in its broad sense), which could be considered as the resilience of the system (Verbesselt et al. 2016).

Similarly, as resistance is defined as the ability to withstand external shocks where highly resistant forests will deviate less than forests with low resistance during perturbations, the depth of the deviation is considered as an indicator of resistance (De Keersmaecker et al. 2014). In addition, growth stability can be measured by calculating the area under the curve of the undecomposed NDVI at a yearly basis and is measured by the inverse of the coefficient of variation (mean divided by the standard deviation) of the respective years of the time series (Isbell et al. 2009).

Apart from quantifying the degree of stability of forests to disturbances, understanding and predicting the effect of environmental factors strengthening or weakening forest stability is little explored (Yan et al. 2011). Therefore, this research aims at quantifying the effect of different explanatory variables describing tree species diversity, local degradation indicators and climate on forest resilience, resistance and growth stability over time using MODIS NDVI time series. Such information will be crucial for planning a successful restoration and forest management (Anjos and De Toledo 2018). With this respect, the study strives to test the following hypotheses: 1) precipitation and temperature play a vital role in the stability of dry forests, 2) topographic and edaphic factors and local land degradation indicators further modulate the difference in the stability of forests, 3) stands with multispecies composition have more growth stability resistance and resilience under climate fluctuation and human disturbances than monocultures.

Methods

Study area description

The study was carried out in Desa'a Forest, a large degraded dry Afromontane forest situated in the Tigray and Afar regions in the north of Ethiopia, for which an ambitious restoration plan is ongoing. The altitudes range from 900 m in Afar lowlands to 3000 m in the highlands of Tigray (Fig. 1). Due to the large difference in topography and long north-south extension along the escarpment, the geologic formation of the forest area is diverse (Asrat 2002). The bedrock in Desa'a Forest is mainly made up of a Precambrian basement in the northern part and the Hintalo limestone dotted with Adigrat Sandstone in the southern landscape (Williams 2016).

The precipitation pattern of the study area is influenced by topography and rain-bearing winds and is dominated by a large inter-annual variability (Nyssen et al. 2005). Data from a nearby meteo-station and Worldclim (http://worldclim.org/version2) (Fick and Hijmans 2017) indicate that the average annual temperature and precipitation of the study area ranges between 13 °C to 25 °C and 400 to 700 mm respectively. Drought has a long history in the area, and caused

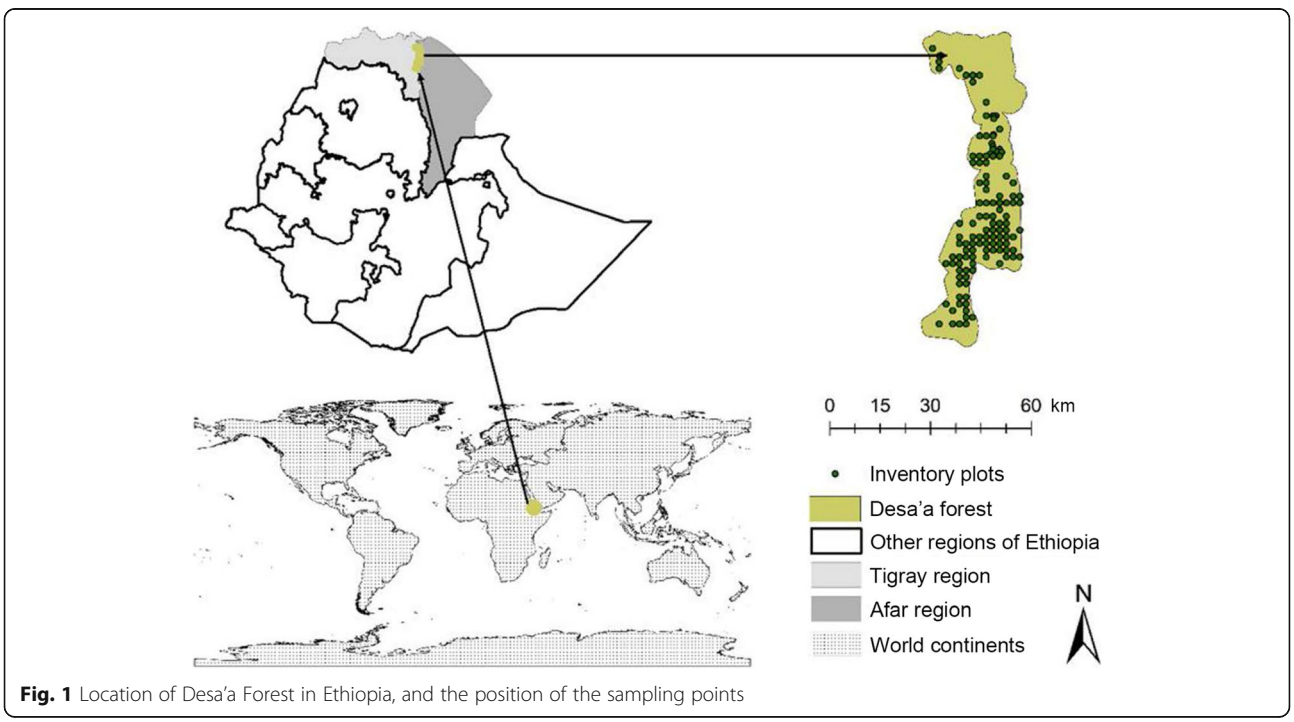

Fig. 1 Location of Desa'a Forest in Ethiopia, and the position of the sampling points

regular famines, including in recent times. Recent droughts have been recorded for 2000, 2002, 2004 and 2009 (Gebrehiwot and van der Veen 2013). In a recent study, 2012 and 2013 were added among the driest years in the region (Tefera et al. 2019).

Desa'a Forest is most often classified as a dry Afromontane forest with a long dry season, where *Juniperus procera* Hochst. ex Endl. and *Olea europaea subsp. cuspidata* (Wall. ex G. Don) Cif. are the dominant species (Friis et al. 2010) in the canopy and understory, respectively. In Aynekulu et al. (2012), dry Afromontane forest (Juniper-Olea-Tarchonanthus group), semi-deciduous shrubland (Cadia-Acacia group), open acacia woodland and semi-desert shrubland (Balanites group) was identified from top to bottom along the altitude gradient. The forest is under strong degradation pressure by livestock and overcutting and is undergoing fast species composition change (Aynekulu et al. 2011)) with a 500 m upward shift in the tree line for juniper and olive species so far (Aynekulu et al. 2011). Desa'a forest covers an area of 150,000 ha.

Data collection

Environmental factors

The ground data were collected by systematic sampling, based on a 2 km by 2 km grid. At each corner of the grids, 303 plots of 400 m^2 were established on which all woody species, shrubs and trees, were identified following the nomenclature of Ethiopian flora (Tesemma 2007) and counted. For each tree, diameter at breast height (DBH) at 1.3 m above ground was measured using a calliper. For shrubs, diameter at stump height (DSH) at 30 cm above ground was measured. Trees with at least 5 cm in DBH and shrubs with at least 1 cm in DSH were considered. Only plots with a vegetation cover above 10% following the FAO definition of forest, 131 plots were used (FAO 2010). For the shrub and tree layers, canopy cover was estimated by a group of three experts and an average was recorded.

For each plot, slope, aspect and altitude were extracted from the 30 m spatial resolution ASTER Digital Elevation Model. The 19 standard Bioclimatic variables for 30 years (1970–2000) were extracted at 1 km resolution from the WorldClim WebPortal (http://worldclim.org/version2) (Fick and Hijmans 2017). The definition and nature of the bioclimatic variables are well documented in Fick and Hijmans (2017) and (O'Donnell and Ignizio 2012).

Distance to nearby settlements and roads were extracted from a Euclidean distance raster constructed from a digitized road and settlement shapefiles. The shapefiles were obtained from a combination of data digitized from Google earth, and GPS tracked major and feeder roads, towns and centre of encompassing villages.

In every plot, local disturbance indicators such as fire incidence, grazing and logging severity were estimated (see appendix 1, supplementary material) following Aynekulu et al. (2011). In each of the diversity inventory plots, soil depth was measured by penetrating a metal rod until the bedrock is reached. The thickness of the forest floor (ectorganic humus layer) was measured after cutting a profile with a spade (Eriksson and Holmgren 1996) (Table 1).

Satellite imagery

Moderate Resolution Imaging Spectroradiometer (MODIS) satellite data, i.e. the global MOD13Q1 data product with a temporal resolution of 16 days and a spatial resolution of 250 m, was used. MODIS NDVI time series from 2001 to 2018 were downloaded from Google Earth Engine (Hird et al. 2017). Upon downloading, low data quality observations such as pixels covered by clouds were masked (Hird et al. 2017). NDVI values were extracted for the pixels covering each inventory plot for every scene as a matrix of bimonthly NDVI over the 18 years in R-software.

Data analysis

Time series decomposition

The time series were decomposed into trend, seasonality and remainder (anomalies) components using Seasonal-Trend decomposition using Loess (STL) (Abbes et al. 2018) in R software. The trend component indicates long-term forest development, while the seasonal component depicts annual growth variations (Quan et al. 2016). The remainder is the difference obtained when the trend and seasonality are subtracted from the original time series (Verbesselt et al. 2016) (Fig. 2).

Deriving ecosystem stability metrics from the NDVI time series

Three stability metrics were used to describe forest dynamics: resilience, resistance, and growth stability. While resilience and resistance were based on the anomalies of the NDVI time series (De Keersmaecker et al. 2014),

Table 1 Categorical environmental factors collected in the field (Lower rank indicates better forest condition and higher values indicate bad forest condition; while soil depth, humus depth and erosion status were assessed into five ranks, grazing, cutting and fire incidence were ranked into four)

Factors	Ranks				
	1	2	3	4	5
Soil Depth (cm)	> 100	75–100	50–75	25–50	0–25
Humus Depth (cm)	> 10	5–10	2–5	0–2	0
Erosion	Absent	Low	Moderate	high	Very high
Grazing	Absent	Low	Medium	High	–
Cutting	Absent	Low	Medium	High	–
Fire incidence	Absent	Low	Medium	High	–

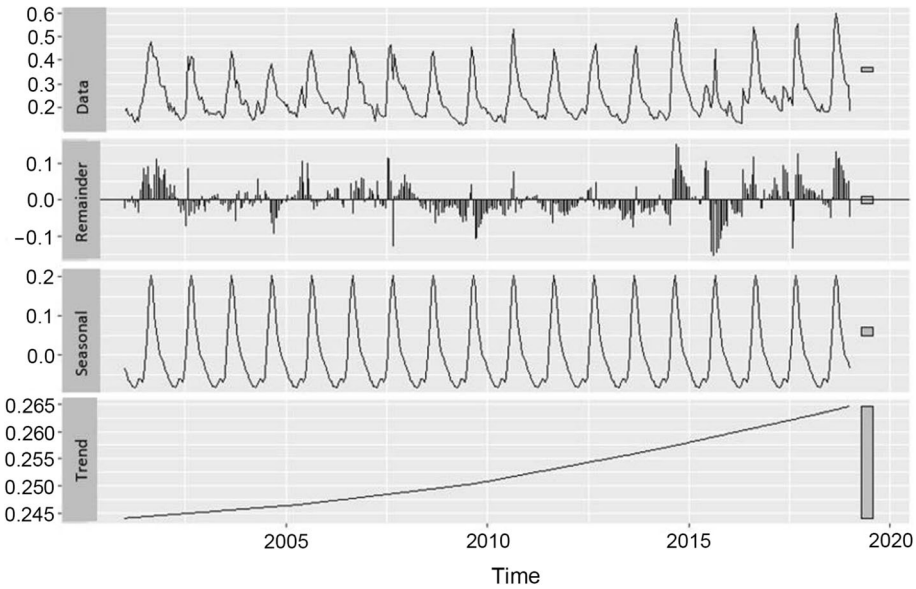

Fig. 2 An example of an NDVI time series of Desa'a forest, study area, decomposed using the STL algorithm

growth stability was based on the integrals of the undecomposed NDVI time series (Isbell et al. 2009).

Resilience Resilience (Fig. 3) was computed using the temporal auto-correlation (TAC) of the anomaly. TAC and resilience are given in the following formula (Dakos et al. 2012), Eqs. 1 and 2, respectively. Highly correlated events (= high TAC) represent a slow recovery rate (= low resilience).

$$\mathrm{TAC} = \frac{\sum_{t=i}^{n-1}\left(X_t - \overline{X}\right)\left(X_{t+1} - \overline{X}\right)}{\sum_{t=1}^{n}\left(X_t - \overline{X}\right)^2} \quad (1)$$

$$\mathrm{Resilience} = 1 - \mathrm{TAC} \quad (2)$$

where TAC is the temporal autocorrelation at lag 1, X_t stands for the observation at time t and n equals the total number of observations.

Resistance The resistance was calculated as the lowest 5th percentile of the remainder (anomalies) per year (De Keersmaecker et al. 2014) (Fig. 3). Small values for the resistance metric represent highly resistant forests, i.e. forests that will deviate to a small extent during perturbations.

Growth stability The growth stability was calculated from the integral of the undecomposed NDVI time series (Yin et al. 2012). The area under the curve of yearly based NDVI time series was considered as a good proxy for the net primary production (growth) of the forest. This area under the curve was obtained based on the top 75% of the yearly NDVI response to avoid the possible effect of seasonal variation in vegetation properties such as leaf sheds (Fig. 4). The growth stability was then calculated as the inverse of the coefficient of variation (i.e. a ratio of mean to standard deviation) of the area under the curve.

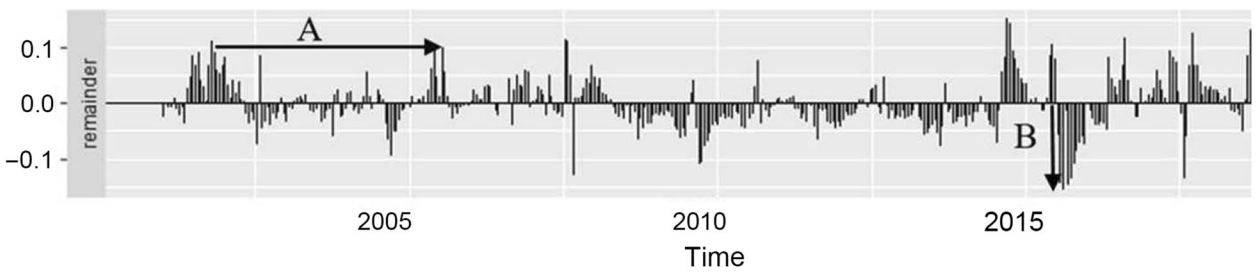

Fig. 3 The concept of resilience (A) resistance (B) as used in this study on the remainder of the time series decomposition. Resilience is the recovery rate of the community, the resistance if the net change in the community

Tree diversity

Basal area (BA) based on species diversity was derived using the Shannon-Wiener diversity index (H') and evenness index (J) equations (Shannon 1948), Eqs. 3 and 4, respectively.

$$H' = \sum_{s=0}^{s} \mathrm{BA}_i \ln (\mathrm{BA}_i)' \quad (3)$$

$$J = \frac{H'}{H' \max} = \sum_{s=0}^{s} \mathrm{BA}_i \ln (\mathrm{BA}_i / \ln(s)) \quad (4)$$

where H' is the Shannon-Wiener diversity index, J is Shannon-Wiener evenness index, and BA_i is the BA proportion (n/N) of individuals of the abundance of the i^{th} species (one particular species) found (n) divided by the total number of individuals found (N) (species richness), and S is the number of species. These diversity indices were later used as explanatory variables in the regression analysis.

Statistical analyses

The four forest stability metrics were modeled against climate, tree species diversity, edaphic and topographic variables and land degradation indicators. Boosted Regression Trees (BRT) was applied as a regression model (Elith et al. 2008) for each metric to explain the dynamics of the forest as a system and identify the most important factors predicting each metric.

BRT allows handling of complex interactions while allowing simplicity for ecological interpretation (Elith et al. 2008; Aertsen et al. 2012). BRT combines the power of regression trees and boosting. It continuously partitions the data into homogeneous parts and fits a specific model to each partition. This avoids the loss of unexplained data if a single regression model could be fitted into such complex interactions. In R-environment, BRT was run using the *gbm.step* function developed by Elith et al. (2008) which as an extension of the "gbm" package (Ridgeway 2007), and explanatory variables could be simplified to concentrate on the most meaningful and important ones using the *gbm.simplify* to boost the power of the model (Elith et al. 2008).

The different variables used in the analyses were checked for multi-collinearity using the variation inflation factor (VIF) and Pearson correlation. Variables with higher VIF (> 5) and Pearson correlation (> 0.7) between predictors were not included in the reported outputs (Aertsen et al. 2012). BRT was run for the different stability metrics by varying the learning rates (0.001–0.05), tree complexity (1–5) and bag fraction (0.50–0.75). Model performance was measured using R-squared, AIC and root mean square error (RMSE). In the BRT, the cross-validation (CV) statistic is the most important measure to evaluate the results (Elith et al. 2008). The cross-validation correlation is the mean correlation of the predicted data iteratively based on the number of folds (Elith et al. 2008). The higher the correlation, the higher the predictive power of the model. Because the algorithm is of a stochastic nature, based on the bag fraction used (the default is 75%), a portion of the data (here 50% was used) is used to train the model and the remaining for prediction capability test. Variable importance is determined by averaging the number of times, a variable is selected in the iterative division (splitting) of data weighted by the squared improvement to the BRT model (Gu et al. 2019). Variables that are above the median of the group in the model value are highly important (significant), and those that are below are less important variables in the model (Gu et al. 2019). Results were also supported by partial dependence plots to ease ecological interpretability of the effect trend of the factors considered.

To generate wall to a wall map of stability metrics over the forest, a kriging interpolation in ArcMap10.6 was

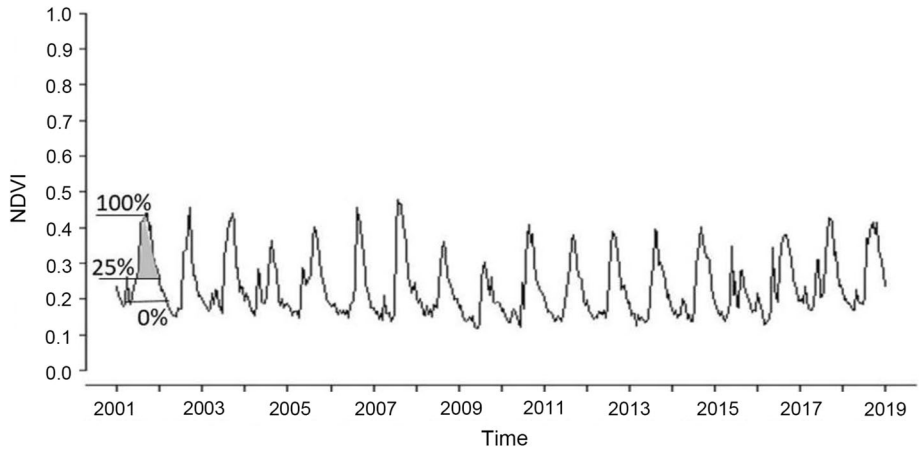

Fig. 4 Fraction of the yearly NDVI (75%) used to extract growth stability for Desa'a forest

applied to the stability metrics obtained on a plot level. Similarly, the stability matrices were summarized on an annual basis to show the stability status of the forest over the study period. A summary of the methodological approach is presented in the flow chart below (Fig. 5).

Results

Stability status of Desa'a forest and correlation of the metrics

The resilience, resistance, and growth stability of Desa'a forest from 2001 to 2018 depict a similar trend (Figs. 5 and 6, Table 2). The resilience index showed lows in the years 2001, 2007 and 2015 (Fig. 6). The resistance showed minima in 2004, 2008, 2009 and 2015. The growth stability, however, was declining throughout the study period except for a sudden rise in 2016 (Fig. 7). Additionally, the spatial distribution of the four metrics showed similar patterns (Fig. 8), where vegetation in the south was more stable while in the center of the study area it was less stable. In the north, however, it was more stable except for the resilience metric.

The correlation between the stability metrics used shows that resilience ($r = 0.56$) and resistance ($r = 0.46$) correlated significantly with growth stability. However, the correlation between resistance and resilience was weak (0.23). The correlation among resilience, resistance and productivity was positive.

Drivers of stability

Drivers of resilience

Resilience was influenced by a combination of biophysical and climatic factors. In general, precipitation of the wettest month, species evenness, distance from the settlement and slope were the most effective variables explaining the resilience of Desa'a forest. The other factors had a similar share of influence (Table 2).

The partial dependencies of the variables in the model indicated that three main types of responses could be observed. First, the precipitation of the wettest month, annual precipitation, annual temperature, Shannon diversity, distance to settlement, and annual temperature range showed a similar trend. Their influence was increasing up to a certain optimal condition and ceiled afterwards. In all except the precipitation of the wettest month, visible reductions in resilience were observed before an ultimate increment was recorded. Second, the effect of both species evenness and slope showed a unimodal shape, high at the mid values and lower at the two ends. Third, temperature seasonality and stoniness showed a negative effect on the resilience of the forest (Fig. 9).

Drivers of resistance

Temperature seasonality and temperature of the driest quarter, forest floor thickness and precipitation of the wettest month were the variables that influenced the resistance of the forest most, with a total contribution of 53.6% (Table 3).

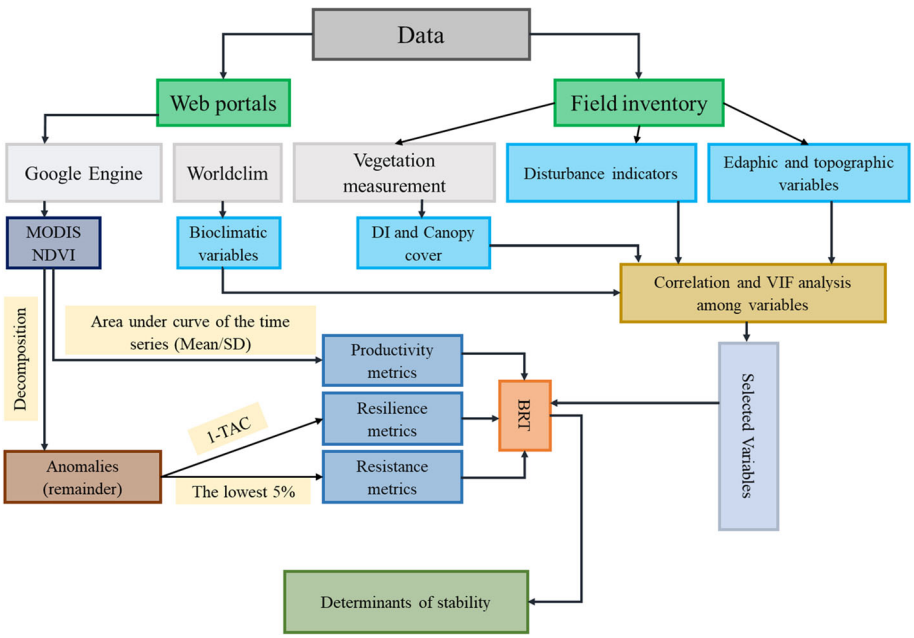

Fig. 5 Methodological flowchart showing the workflow used in this paper. DI is Diversity indices, VIF is variance inflation factor, TAC is temporal autocorrelation, SD is the standard deviation, and BRT is boosted regression tree. Same colours show similar work stages; blue represents final input variables and green data sources, for example

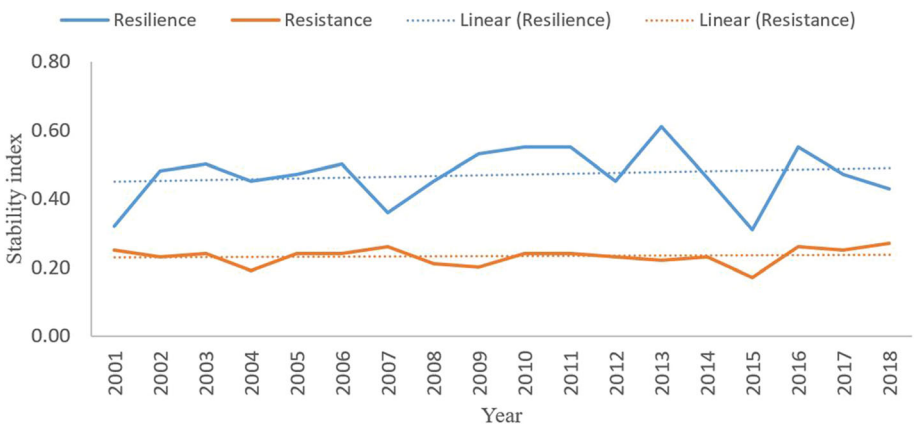

Fig. 6 The NDVI derived resilience and resistance of Desa'a Forest between 2001 to 2018. The solid line is the average of each metrics of all plots in a particular year and the broken line is the linear trendline of each metric

The partial dependency plots revealed that the important variables affecting resistance had two general effect trends. First, the influence of temperature seasonality ended up in a decreasing trend though they showed different responses in the process. The resistance of the forest was lower in areas where temperature seasonality was lower than 180 (1.8 °C), the optimal size of temperature seasonality and got pick at around 220 (2.2 °C) above which an increase in temperature seasonality resulted in reduced resistance of forest communities. Second, the effect of the mean temperature of the driest quarter, humus depth and precipitation of the wettest month followed a positive trend. Around 185 mm precipitation of the wettest month is optimal to keep a resistant forest in the dry Afromontane environment (Fig. 10).

Drivers of growth stability

Growth stability was governed dominantly by precipitation of the wettest month, taking about 44% of the total effect. Annual temperature range, precipitation of the warmest quarter and distance to settlement had similar effect strength accounting for 56% of the total (Table 4).

The partial dependencies of the factors influencing growth stability (Fig. 11) show that the stability of the forest has been increasing with all the important factors. However, the increment rate was different across the factors. The growth stability remained low up to around 155 mm of precipitation of the wettest month, and it exponential increased and ultimately ceiled at 180 mm (Fig. 11).

Model strength of the different stability metrics

The performance of the model fit to the different stability metrics is given in Table 5. Modelling growth stability with the variables used was difficult compared to the other response variables, resulting in the lowest performance for all goodness-of-fit criteria used (Table 5).

Discussion

Resilience, resistance and growth stability status of Desa'a forest

Over the study period, Desa'a Forest remained more or less resistant but not resilient, with a significant decrease in resilience in 2001, 2007 and 2015. A slight drop below the average resistance was also observed in 2004, 2008,

Table 2 The relative influence of the variables determining resilience in Desa'a forest (in bold are significant factors)

Variable	Relative influence (%)	Optimal value
Precipitation of the wettest month	**15.7**	**175 mm**
BA Evenness	**12.9**	**0.7**
Distance from a settlement	**12.8**	**5 km**
Slope	**10.9**	**18 degrees**
Annual precipitation	10.1	650 mm
Shannon diversity index	9.9	1.5
Temperature seasonality	9.5	1.8 °C
Temperature annual range	9.3	22.5 °C
Stoniness	8.9	10%

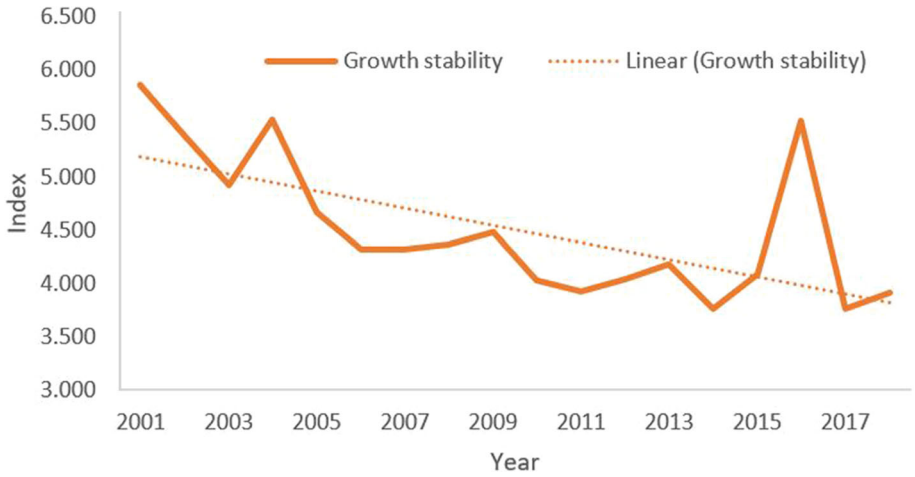

Fig. 7 Growth stability in Desa'a Forest, 2001 to 2018. The solid line is the average growth stability of all plots in a particular year and the broken line is the linear trend of the growth stability

2009, and 2015. The frequent, and acute drought occurrences might explain these drops in both resilience and resistance in the region. In the study period, reported droughts occurred in 2000, 2002, 2004 (Gebrehiwot and van der Veen 2013), 2012 and 2013 (Tefera et al. 2019), and 2015 (Ahmed et al. 2017). The resilience range of Desa'a forest (0.3–0.6) is incomparably lower than that of other African tropical forests (0.7–1.0) reported by Verbesselt et al. (2016) which might explain the severe and repetitive anthropogenic pressure the forest is facing (Aynekulu et al. 2011). The growth stability, however, was continuously decreasing over the study period, which might be linked to continuous degradation in the forest that could be explained by the dieback of the dominant species, olive and juniper trees (Aynekulu et al. 2011), browsing and lopping of various species (Giday et al. 2018). The frequent drought occurrences that were linked to the declined resilience of the forest

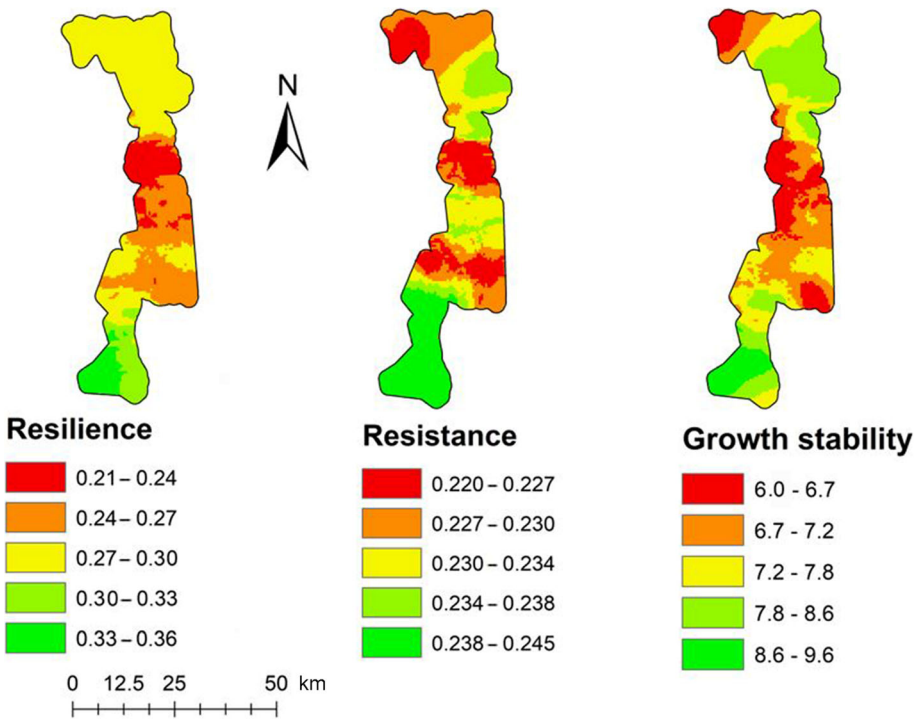

Fig. 8 Spatial distribution of resilience, resistance, and growth stability in Desa'a Forest

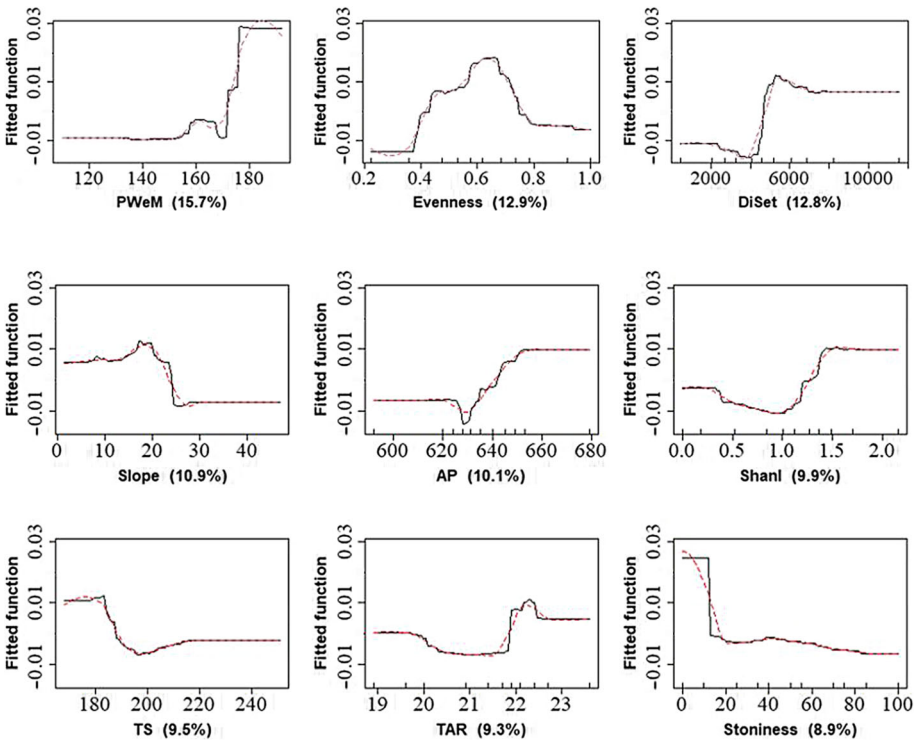

Fig. 9 Partial dependencies of factors affecting resilience in Desa'a forest. The relative importance of variables in the model (% out of 100) is given in brackets. Fitted functions are centred around the mean of the resilience and plotted on a common scale. Rug plots (ticks in *X*-axis) show the distribution of sample measurements. PWem stands for precipitation of the wettest month, DiSet for distance from the settlement, AP for annual precipitation, Shanl for Shannon index, TS for temperature seasonality and TAR for temperature annual range

might also be a reasonable explanation for the decreased yield stability. A clear increment of growth was, however, observed in 2016. This might be attributed to the increased rainfall recorded in 2016 (Berhane et al. 2020). Because there was an acute drought in 2015 (Ahmed et al. 2017) and significant increment in precipitation in 2016, growth might have positively affected the biomass production in the forest.

Among the determinants of resilience, resistance, and growth stability, those above the median in the contribution of the factors are considered important (significant) factors (Gu et al. 2019) and are discussed.

Drivers of forest resilience

Precipitation of the wettest month was the most important factor associated with resilience. Although dry forests in the tropics are generally considered more resilient, their recovery is heavily dependent on the amount of precipitation (Álvarez-Yépiz et al. 2018), which is in line with the results of this study. A similar result was also reported in a wide range of tropical forest ecosystems where extended drought and low precipitation slows the recovery of forests in different continents (Verbesselt et al. 2016) and Amazon mountain forests (Nobre and Borma 2009).

Table 3 The relative influence of the variables determining resistance in Desa'a Forest (in bold are significant factors)

Variables	Relative importance (%)	Optimal value
Temperature seasonality	**19.4**	**2.2 °C**
Mean temperature of the driest quarter	**19.3**	**20 °C**
Humus depth	**14.9**	**2 cm**
Precipitation of the wettest month	**13.9**	**185 mm**
Temperature annual range	10.9	21.5 ℃
Stoniness	10.8	30%
Isothermality	10.7	72%

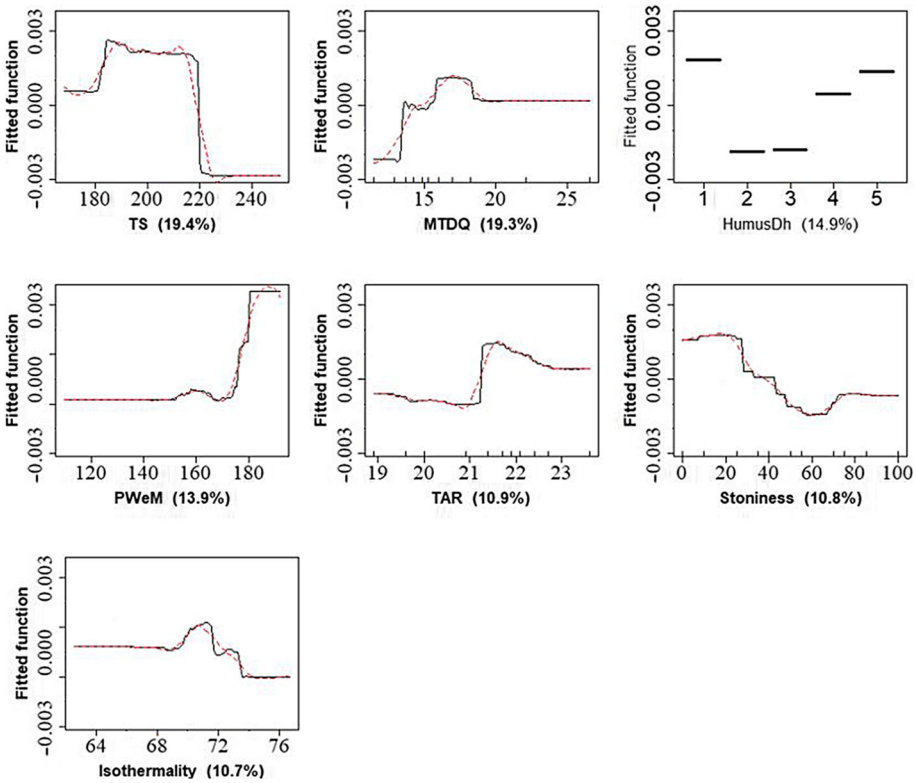

Fig. 10 Partial dependencies of factors affecting resistance in Desa'a forest. The relative importance of variables in the model (% out of 100) is given in brackets. Fitted functions are centred around the mean of the resilience and plotted on a common scale. Rug plots (ticks in *X*-axis) show the distribution of sample measurements. TS stands for temperature seasonality, MTDQ for a mean temperature of the driest quarter, HumusDh for humus depth, PWeM for precipitation of the wettest month, and TAR for temperature annual range

Generally, tree diversity was associated with resilience, yet the Shannon and evenness indicators had a different impact. In the literature, there are contradicting findings on the effect of diversity on stability, where positive effect of species diversity has been reported in grasslands (Tilman et al. 2006; Van Ruijven and Berendse 2010), and in forests across Europe (Guyot et al. 2016, Sousa-Silva et al. 2018, Vannoppen et al. 2019), while others argue that there is no true positive diversity effect found so far on resilience (Bauhus et al. 2017). We found a positive association of Shannon diversity with resilience, but saturating eventually. The positive effect of diversity on resilience might be explained by the insurance effect where different species respond differently to disturbances stabilizing the overall resilience as a system regardless of the lowered performance of certain member species (Loreau 2004). However, the effect of evenness was unimodal, with the highest evenness values resulting in a lower forest resilience. In this forest, dominant species might be needed to some extent to keep the forest community more resilient. Such species could have particular functional traits that play a significant role in the stability of the forest community (Yan et al. 2011). However, diversity indices lack information to indicate the functional role of species (Yan et al. 2011) and limit the identification of the species that are disadvantaged when sites get more even. In Desa'a Forest, such late successional species could be those that are less competitive such as juniper tree (Alshahrani 2008), which are disadvantaged when they grow in even proportion to others, reducing the total resilience of the forest community.

Table 4 The relative influence of the variables determining growth stability in Desa'a forest (in bold are significant factors)

Variable	Relative influence (%)	Optimal value
Precipitation of the wettest month (PWeM)	**43.52**	**175 mm**
Temperature annual range (TAR)	**20.52**	**22.5 °C**
Precipitation of the warmest quarter (PWaQ)	19.25	240 mm
Distance to settlement (DiSet)	17.61	6000 m

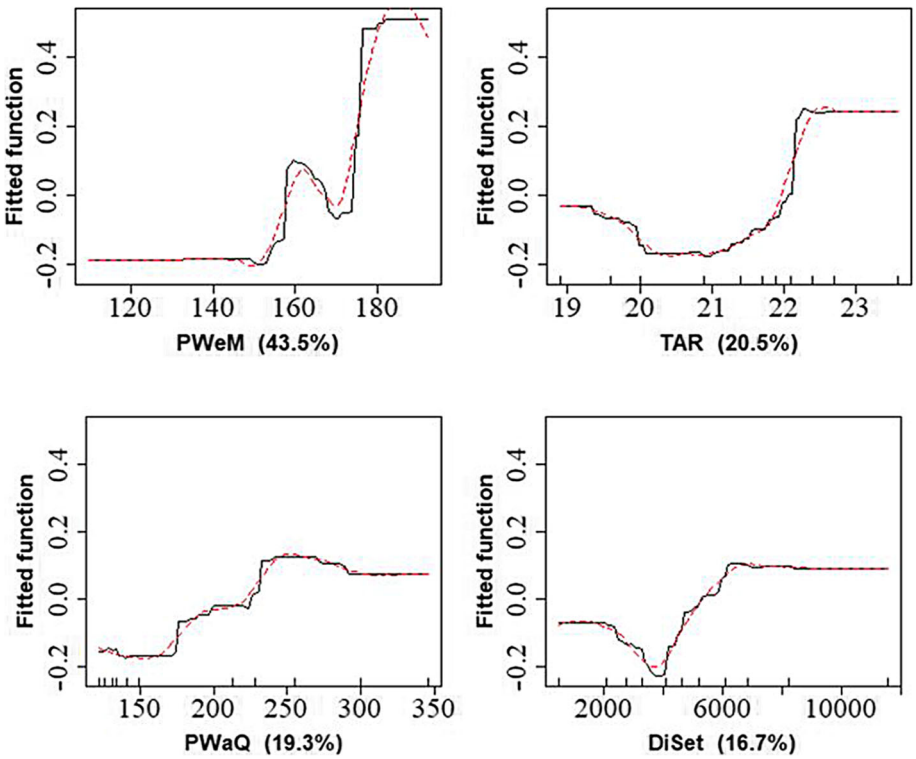

Fig. 11 Partial dependencies of factors affecting growth stability in Desa'a forest. The relative importance of variables in the model (% out of 100) is given in brackets. Fitted functions are centred around the mean of the growth stability and plotted on a common scale. Rug plots (ticks in *X*-axis) show the distribution of sample measurements. PWeM stands for precipitation of the wettest month, TAR for temperature annual range, PWaQ for precipitation of the warmest quarter and DiSet for distance to settlement

Proximity to a settlement increases the probability of anthropogenic disturbance such as grazing and cutting, which are predominant in the forest (Giday et al. 2018). Our results confirm that the resilience of the vegetation located further than 5 km from settlements was considerably increased. The anthropogenic disturbance could affect resilience by affecting species composition, which might introduce an artificial dominance of a certain tree species and reduce species richness. That could have a direct impact on the resilience of the forest (Hillebrand et al. 2008).

The negative effect of slope on the resilience might be linked to its effect on soil depth, moisture content and susceptibility to degradation where steep slopes and exposed rocky areas have a little medium for plant growth due to erosion (Zhang et al. 2015), and when disturbances prevail, they are more affected than those in good soil conditions and gentle slopes. In general, in line to our hypotheses, the combination of tree diversity, local human impact, topographic position and climate (mainly precipitation) controlled resilience in dry Afromontane forest.

Table 5 Stability metrics and their model performance (TDC is training data correlation, CVC is cross-validation correlation)

Criteria	Resilience	Resistance	Growth stability
RMSE	0.04	0.01	1.60
R^2	0.74	0.6	0.38
AIC	−395	− 577	65
TDC	0.86	0.78	0.60
CVC	0.32	0.34	0.20

Drivers of resistance

While temperature seasonality was negatively associated with resistance, mean temperature of the driest quarter, humus thickness and precipitation of the wettest month was positively associated. In contrary to resilience, the resistance of forests is dependent more on their productivity before a disturbance (Wang et al. 2007; Van Ruijven and Berendse 2010). Therefore, forest communities growing in productive sites, having favourable environmental conditions, are expected to show higher resistance (Wang et al. 2007). In line with this argument, our results indicated that vegetation growing in sites with thicker humus and more stony sites had higher and lowered resistance, respectively. The negative effect of increased temperature seasonality on forest resistance might be a general attribute to the tropical forests which have developed themselves under relatively stable

climatic conditions (Blach-Overgaard et al. 2010). Therefore, in response to their narrow climatic tolerance, as the seasonality of temperature increases, forests might lose the capacity to rearrange (to adapt quickly) themselves so reducing their resilience capability (Blach-Overgaard et al. 2010). Our results indicate that higher temperature seasonality and annual temperature range were associated with lower resistance. In the highland parts of Desa'a Forest, where it is relatively colder and dominated by climax species, a negative correlation between temperature and growth of juniper and olive trees was reported (Mokria et al. 2017; Siyum et al. 2019). Temperature seasonality between 1.8 °C and 2.2 °C and an annual temperature range between 21 °C and 22 °C were associated with higher resilience. Increased temperature seasonality and annual temperature range prolongs the disturbance and slows the recovery and break the resistance (Anjos and De Toledo 2018) due to increased fluctuation and excessive evapotranspiration (Schroth et al. 2009).

In contrast to the resilience indicator, no association between biodiversity and resistance could be found. This is in line with the findings of Van Ruijven and Berendse (2010) who reported the positive effect of biodiversity on community resilience after a drought, but there was no association found with resistance. This is another strong evidence that resistance to disturbance depends on a prior forest condition (production, health, etc.). In contrast, the post-disturbance response of the forest could be supported by its constituents, such as diversity (Van Ruijven and Berendse 2010). While our hypothesis on the positive effect of climate and good edaphic properties on resistance holds true, the effect of tree diversity was not supported by our results.

Drivers of growth stability

The growth stability was mainly controlled by climate, the precipitation of the wettest month. The effect of tree diversity was not observed, and only the distance to settlement as an indicator of human impact indicator was detected though not significant. In dry forests, precipitation is the most important factor for the growth of trees and increased biomass (Hiltner et al. 2016). Dry forests are affected by high evapotranspiration due to the high temperature and low precipitation (Souza et al. 2016), and when precipitation gets higher, the growth of the forests is positively affected. The results are in line with the findings from different tropical forests; subtropical forest in China (Gu et al. 2019), dry tropical montane forests of Ethiopia (Hiltner et al. 2016), and in the dry Afromontane forests (Gebru et al. 2020). Effect of anthropogenic disturbances can be mediated and suppressed by the effect of precipitation which initiates more growth and system repair in forests (Rito et al. 2017), which could be the reason for the non-significant effect of disturbance on the growth stability of this forest.

The relationship among resilience, resistance and growth stability in Desa'a forest

Forest stability was successfully characterized using resilience and resistance from remotely sensed imagery in different forests (Sousa-Silva et al. 2018; Frazier et al. 2018). In Desa'a, a dry tropical Afromontane forest, the three stability metrics were modeled. The correlation analysis between the metrics showed that the correlation between resilience and resistance was very weak but positive. This is in line with the concept of DeRose and Long (2014), who argued that resistance and resilience act upon ecosystems differently. While resilience is related to the influence of disturbance on the structure and composition of the ecosystem, resistance is related to the influence of the structure and composition of an ecosystem on disturbance. In support of our results, Gazol et al. (2018) reported low resistant forests to be more resilient across different biomes. Against our findings, a negative correlation was found between resistance and recovery rate from another tropical dry forest (Bhaskar et al. 2018). The difference in the correlation results might be due to the difference in the interaction of climate and local degradation factors (Bhaskar et al. 2018).

Conclusion and recommendation

The dry Afromontane forest of Desa'a was generally resistant but less resilient experiencing a continuous decline growth in stability in the last two decades. Climate variability played a pivotal role in the resilience, and resistance of the forest. While the precipitation of the wettest month is the most important factor in all the stability metrics, an inter-annual variation above 2 °C is was enough to degrade the resilience and resistance of the forest. Furthermore, tree species diversity was important to enhance the resilience of the dry Afromontane forest, but no evidence of tree diversity effects was found for resistance and growth stability. We found a threshold (0.7), above which tree species evenness leads to less resilience. Experimental research might be important to investigate into what extent of evenness species identity is important to promote resilience in the dry forests. Moreover, distance to the settlement, which is an indicator of degradation and slope were also important to promote resilience. Climate, both precipitation and temperature, edaphic factors, local human disturbance indicators and tree diversity were important for one or all of the stability metrics investigated in the dry Afromontane forest.

Supplementary Information

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Additional file 1 : **Appendix 1**. Methodological protocol for humus, soil depth, and local human disturbance indicators assessment.

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Authors' contributions

Conceptualization: HH & BM; Methodology: HH & BM; Formal Analysis: HH & LO; Writing – original draft: HH; Writing review & editing: BM, BS, WD & KG; Supervision: BM. The author(s) read and approved the final manuscript.

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Availability of data and materials

The datasets generated during and/or analyzed during the current study are available in the KU Leuven repository, and are accessible according to the regulation of the University.

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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