Discerning effects of climate variability, local land degradation and tree species diversity on remote sensing derived resilience and resistance of dry Afromontane forest

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Abstract

**Introduction:** 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, but 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, resistance and variability 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 disturbance, obtained from a systematic grid of field inventory plots, using boosted regression trees in R. Resilience and resistance were adequately predicted by these
factors with an R\(^2\) of 0.67 and 0.48, respectively, but the models for variability and growth stability were 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 significant, 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.

**Conclusion:** A combination of climate, topographic variables and disturbance indicators controlled the stability of the dry forest. Tree diversity is an important 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

1. **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 1,079 million ha (Bastin et al. 2017), accounting for almost half of the (sub)tropical forests (Aide et al. 2013). Dry forests provide important ecosystem services,
including the provision of shade, moisture, pollinators, nutrient protection, runoff and soil erosion reduction, and carbon sequestration (Safriel et al. 2005).

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). 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).

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, resistance and variability have been used widely (De Keersmaecker et al. 2018; Verbesselt et al. 2016). 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). Variability is another metric that evaluates how the anomalies vary from the mean (De
Keersmaecker et al. 2018). 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), 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).

Several approaches can be used to derive forest stability metrics from NDVI time series, among which the holistic approach (Verbesselt et al. 2016; Hutchison et al. 2018). The holistic approach considers the whole time series of a study period and originates from the idea that in a natural environment, stochastic perturbation events such as drought and other environmental variations are recurrent (Verbesselt et al. 2016). Therefore, a continuous evaluation of the forest response to those fluctuations can be captured by applying statistical methods to the whole time series (Verbesselt et al. 2016). 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, resistance and variability, 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).

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, variability 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 less variability under climate fluctuation and human disturbances than monocultures.
2. Methods

2.1. 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 to 25 °C and 400 to 700 mm respectively. Drought has a long history in the area, and caused 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).

Figure 1 Location of Desa’a Forest in Ethiopia, with the position of the sampling points along the altitudinal gradient of the study area
2.2. Data collection

2.2.1. Environmental factors

The ground data were collected by systematic sampling, based on a 2 by 2 km grid. At each corner of the grids, plots of 400 m² 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 using a calliper. For shrubs, diameter at stump height (DSH) at 30 cm above ground was measured. Only plots with a vegetation cover above 10% following the FAO definition of forest 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).

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 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).
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 | -     |

**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.
2.3. Data Analysis

2.3.1. 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). 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).

![An example of an NDVI time series of Desa’a forest, study area, decomposed using the STL algorithm.](image)

Figure 2 An example of an NDVI time series of Desa’a forest, study area, decomposed using the STL algorithm.
2.3.2. Deriving ecosystem stability metrics from the NDVI time series

Four stability metrics were used to describe forest dynamics: resilience, resistance, variability, and growth stability. While resilience, resistance and variability were based on the anomalies of the NDVI time series (De Keersmaecker et al. 2014), 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), equation 1 and 2, respectively. Highly correlated events (= high TAC) represent a slow recovery rate (= low resilience).

\[
TAC = \frac{\sum_{t=1}^{n-1} (x_t - \bar{x})(x_{t+1} - \bar{x})}{\sum_{t=1}^{n} (x_t - \bar{x})^2} \quad \text{Equation 1}
\]

\[
Resilience = 1 - TAC \quad \text{Equation 2}
\]

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.

Variability

The variability metric was calculated as the standard deviation of the anomalies (Pimm 1984) (Fig. 3).

Figure 3 The concept of resilience (A) resistance (B) and variability (C) 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 and variability is the standard deviation of the fluctuation in the community due to stressors.

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.

\[ H' = \sum_{s=0}^{s} BA_i ln (BA_i) \]  

\[ J = \frac{H'}{H'_{max}} = \sum_{s=0}^{s} BA_i ln (BA_i / ln(s)) \]

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.
number of species. These diversity indices were later used as explanatory variables in the regression analysis.

2.4. Statistical analyses

The four forest stability metrics were modelled as a function of 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 (0.5 - 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 see how each variable affects the trend of each stability metric, which helps ecological interpretability.

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

3. Results

3.1. Stability status of Desa’a forest and correlation of the metrics

The resilience, resistance, variability and growth stability of Desa’a forest from 2001 to 2018 depict a similar trend (Fig. 5 & 6, Table 2). The resilience index showed lows in the years 2001, 2007 and 2015 (Fig. 5). The resistance showed minima in 2004, 2008, 2009 and 2015. The variability showed peaks in 2001, 2007, 2015 and 2017. The growth stability, however, was declining throughout the study period except for a sudden rise in 2016 (Fig. 6). Additionally, the
spatial distribution of the four metrics showed similar patterns (Fig. 7), 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.

Figure 5 The NDVI derived resilience and resistance (left scale) and variability (right scale) 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.
Figure 6 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.

Figure 7 Spatial distribution of resilience, resistance, variability and growth stability in Desa’a Forest
The correlation between the stability metrics used shows that resilience correlated significantly with both variability (-0.46) and growth stability (0.56). Similarly, resistance correlated with both variability (-0.88) and growth stability (0.46). However, the correlation between resistance and resilience was weak (0.23). (Table 2).

Table 2 Correlation of stability metrics in Desa’a forest.

|                | Resilience | Resistance | Variability |
|----------------|------------|------------|-------------|
| Resistance     | 0.23       |            |             |
| Variability    | -0.40      | -0.88      |             |
| Growth stability| 0.56       | 0.46       | -0.63       |

3.2. Drivers of stability

3.2.1. 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 3).

Table 3 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    |
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 (the temperature difference between the maximum temperature of the warmest and the minimum temperature of the coldest month of a year) 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).
Figure 8 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, ShanI for Shannon index, TS for temperature seasonality and TAR for temperature annual range.
3.2.2. 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 4).

Table 4 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°C        |
| Stoniness                     | 10.8                    | 30 %          |
| Isothermality                 | 10.7                    | 72%           |

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 gets 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).
Figure 9 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.
3.2.3. **Drivers of variability**

The variability was derived dominantly by climatic variables such as the mean temperature of the driest quarter and precipitation of the wettest month, which cumulatively accounted for about 78% of the total relative influence (Table 5).

Table 5 The relative influence of the variables determining variability in Desa’a forest (in bold are significant factors)

| Variable                                | Relative influence (%) | Optimal value |
|-----------------------------------------|------------------------|---------------|
| Mean temperature of the driest quarter | 47.43                  | 10 °C         |
| Precipitation of the wettest month      | 30.26                  | 185 mm        |
| Humus depth                             | 22.31                  | 2 cm          |

The partial dependency of the factors indicated that variability was negatively related to all three factors. However, the effect trend was different. The effect of the mean temperature of the driest month was decreasing and ceiling at around 19°C. Similarly, variability remained high up to the point where the precipitation of the wettest month reaches about 150 mm and drastically reduced afterwards (Fig. 11).

Figure 10 partial dependencies of factors affecting variability 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 variability and plotted on a common scale. Rug plots (ticks in X-axis) show the distribution of sample measurements. MTDQ stands for a mean temperature of the driest quarter, PWeM for precipitation of the wettest month and HumusDh for humus depth.

3.2.4. 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 5).

Table 6 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        |

The partial dependencies of the factors influencing growth stability (Fig. 9) 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. 12).
3.3. **Model strength of the different stability metrics**

The performance of the model fit to the different stability metrics is given in Table 7. 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 7).
4. Discussion

4.1. Resilience and resistance 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, 2009, and 2015. These drops in both resilience and resistance might be explained by the frequent and acute drought occurrences 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 might also be a reasonable explanation for the decreased yield stability.

Growth stability and variability were significantly correlated to both resilience (r= 0.56 & -0.46, respectively) and resistance (r= 0.44 & -0.88, respectively) (Fig.10). Therefore, only the determinants of resilience and resistance were discussed. Similarly, among the determinants of resilience and resistance, those that are above the median in the contribution of the factors are considered as important (significant) factors (Gu et al. 2019) and are discussed.

4.2. Drivers of forest resilience and resistance
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).

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). The effect of evenness was, however, 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.

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.
**Derivers 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 hummus 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 and 2.2 °C and an annual temperature range between 21 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).

4.3. The relationship among resilience, resistance, variability and growth stability in Desa’a forest

Forest stability was successfully characterized using resilience, resistance and variability 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 four stability metrics were modelled. 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 resilience 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). Our results revealed that variability was inversely correlated to resistance, resilience and growth metrics which is in line with the results from a forest in Scotland (Chen et al. 2019).
5. Conclusion and recommendation

In the dry Afromontane forest of Desa’a climate variability is playing a pivotal role in both resilience and resistance of the forest: an inter-annual variation above 2°C is enough to degrade the resilience and resistance of the forest. Furthermore, precipitation and tree species diversity are important variables to enhance the resilience of the dry Afromontane forest. However, we found a threshold (0.7), above which tree species evenness leads to less resilience due to increasing competition, but it remained better than in monoculture stands. Therefore, keeping the balance of species mixture is important and identifying the specific species that are disfavored by a more even distribution of species remains a valid gap of research to consider in the future. Moreover, distance to the settlement, which is an indicator of degradation was also among the important factors determining resilience. While areas in higher altitude with better rainfall and more stable temperature were expected to be more resilient and resistant to disturbances, they exhibited the opposite. The degradation is more severe in the more fertile and accessible highland zone of the forest. Consequently, the resilience and resistance of the vegetation in this zone are very low making it more vulnerable to a possible regime shift in the ecosystem.

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- Ethics approval and consent to participate:
  Not applicable

- Consent for publication
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- Availability of data and material:
  The datasets generated during and/or analyzed during the current study are available in the KULeuven repository, and are accessible according to the regulation of the University.

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