# F+E-Vorhaben des BfN

# „WildesOffenland“

## Bedeutung und Implementierung von „Störungen“ für den Erhalt von Offenlandökosystemen in ansonsten nicht gemanagten (Schutz-) Gebieten

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Simulationsstudie „Kalk-Buchenwald“:

Ergebnisse zu Interaktionen zwischen

Herbivoren, initialer Waldöffnung und Wildfeuer

in der Landschaftsentwicklung im Klimawandel

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# 1 Methods

## 1.1 Study area

To represent beech forest on limestone in artificial model landscapes, data from the national park "Hainich" (Thüringen, Germany) was used. This national park was founded in 1997. The national park (7.500 ha) is integrated in one of the largest continuous deciduous forest areas in Germany (13.000 ha, 51° 5´48° N, 10° 23´27° E). It represents a typical collin to submontane landscape with an annual mean precipitation rate of 600 to 800 mm and a beech (*Fagus sylvatica*) dominated forest. The bedrock is shell limestone with depositions of loess.

The national park is a former military training ground that represents a mosaic of (military)-disturbed forest, open landscape and natural close forest areas (40 years free succession, no forestry). The open landscape area is a patch-mosaic with marginal patches of sandy grasslands, larger patches of fallow and patches of encroachment with shrubs and trees (progressive tree succession is high). For maintenance of the open landscape sheep grazing takes place. There is an increasing amount of dead wood. However, according to the forest community and structure the forest is at a state of "early" natural development. Although there have only been marginal forestry activities in the last 40 years and the last clear cutting was in 1998.

From the common habitat types in the national park „Hainich", the following are relevant in relation to large herbivore, natural wildfire and climate change influences, investigated in this study:

- Natura code (*) 6210 semi-natural dry grasslands and scrubland facies on calcareous substrates
- Natura code *9180 Tilio-Acerion of slopes, screes and ravines
- Natura code 9130 Asperulo-Fagetum beech forests
- Natura code 9150 Medio-European limestone beech forests of the Cephalanthero-Fagion
- Natura code 9170 Galio-Carpinetum oak-hornbeam forests

In regards to common large herbivores, there is a high density of red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*) and fallow deer (*Dama dama*). Besides high densities of wild boar (*Sus scrofa*). There are no natural predators like wolves, lynx or bears.

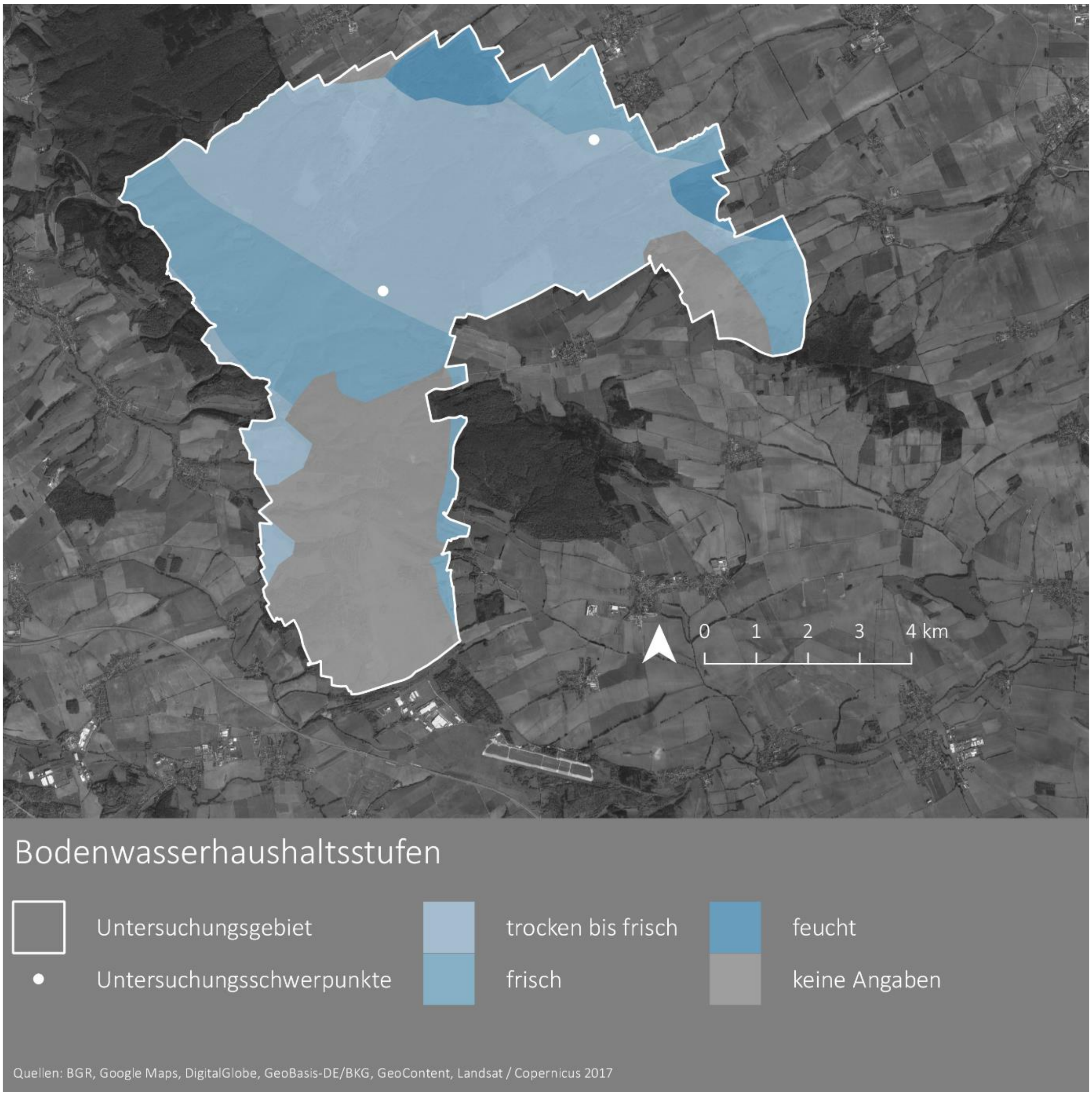



Figure 1 Ranks of soil water content in the national park “Hainich”. Ranks are classified according to the available field capacity at one meter below ground surface in volume (%) fc1m: <6 = dry; 6 - <14 = dry to fresh; 14 - <22 = fresh; 22 - <30 = moist; >30 moist to wet. The zonation corresponds to the edaphic conditions in the artificial model landscapes (main document, Figure 16). References: Nutzungsdifferenzierte Bodenübersichtskarte 1:1000000 (Bundesanstalt für Geowissenschaften und Rohstoffe (BGR)); Luftbild: (NES/Airbus, DigitalGlobe, GEODIS Brno, Geobasis DE/BKG, GeoContent, Landsat/Copernicus).

Table 1 Profile data of the soil entities in the national park “Hainich” (classification of soil entities see Figure 1). Reference data from the Bundesanstalt für Geowissenschaften und Rohstoffe (BGR).

| 350623821 | |
|---|---|
| Topsoil | |
| Depth | fc |
| 0-30 | 22 |
| 30-70 | 26 |
| 70-90 | 26 |
| 90-150 | 24 |
| 150-200 | 10 |
| Ø to 1m | 25 |

| 340724231 | |
|---|---|
| Brown soil | |
| Depth | fc |
| 0-5 | 25 |
| 5-90 | 20 |
| 90-200 | 5 |
| Ø to 1m | 19 |

| 350624021 | |
|---|---|
| Top soil - Para-brown | |
| Depth | fc |
| 0-30 | 18 |
| 30-70 | 18 |
| 70-80 | 13 |
| 80-90 | 20 |
| 90-200 | 22 |
| Ø to 1m | 18 |

| 340725121 | |
|---|---|
| Brown-Pelosol | |
| Depth | fc |
| 0-25 | 18 |
| 25-35 | 10 |
| 35-80 | 8 |
| 80-200 | 8 |
| Ø to 1m | 11 |

| 340725131 | |
|---|---|
| Brown-Pelosol | |
| Depth | fc |
| 0-5 | 22 |
| 5-15 | 20 |
| 15-40 | 15 |
| 60-60 | 4 |
| 60-200 | 0 (Rock) |
| Ø to 1m | 8 |

| | |
|---|---|
| 340724232 | No data |
| 340725132 | |

## 1.2 Delineation of habitat types in the model landscape and quantification of their spatial distribution

Tree cover determines essential habitat qualities in semi-open landscapes. Phytosociological analysis by Gallandat et al. (1995) delivered thresholds for tree cover that define five habitat types ranging from unwooded to forest (Table 2). Following our approach in the Döberitzer Heide, we split the class range of 20 to 70% tree cover into two classes (medium and densely wooded). The enhanced resolution improved the demonstration of both forest thinning processes and progressive succession and of patterns of forest-grassland ecotones in our simulation results.

Table 2 Structural definition of habitat types based on tree cover classes for the analysis of simulation results. The keywords for citation in the text are in bold. Thresholds were defined after phytosociological analysis by Gallandat et al. (1995)

| Habitat | Structural definition |
|---|---|
| 1 | **Unwooded habitat** with tree cover ranging from 0 to 2%. |
| 2 | **Sparsely wooded habitat** with tree cover ranging between 2% and 20%, trees or bushes being mostly scattered. |
| 3 | **Semi-open habitat** with tree cover ranging between 20% and 50%, trees or bushes being scattered or clustered in thickets. |
| 4 | **Densely wooded habitat** with tree cover ranging between 50% and 70%, with trees mostly clustered in thickets. |
| 5 | **Forest** with tree cover higher than 70%, appearing as forest with a closed canopy. |

The identification of distinct habitat types was the pre-requisite for the assessment of the landscape structural diversity. Here we used the landscape aggregation index (He et al. 2000) that quantifies aggregated (clumped) and disperse habitat distributions.

## 1.3 Modelling work, calibration and plausibility checks

We applied the same version of the WoodPaM-model to all study areas. For details refer to the study “Eichenmischwald-Heide-Komplex” (Anhang 3). For the purpose of the Hainich, we newly implemented tree species (chapter 1.3.1) and a threshold for fire ignition in dense beech forest (chapter 1.3.6).

### 1.3.1 Calibration to local climate and reproduction of the current forest community

Previous studies with the WoodPaM-model performed in calcareous subalpine pasture-woodlands with sub-oceanic climate. The transfer of WoodPaM to the study site required some adaptation.

**Reproduction of current forest community**

We had to establish the growth parameters of ash *(Fraxinus excelsior)*, which was not present in previous study sites, and had to calibrate the growth parameters of maple *(Acer pseudoplatanus)* to lower elevations. In contrast to the Döberitzer Heide, we did not consider the tree species-specific rooting depth in the Hainich. On the shallow Rendzina-soil, rooting depth does not determine the tree species’ response to drought in the way as it the case on loose substrate (the case of the Döberitzer Heide). We calibrated the monthly estimates of potential and actual evapotranspiration to observed data following the approach that was developed in the Döberitzer Heide. Both parameters are fundamental in the computation of the drought stress index for tree growth and establishment.

**Calibration of ash *(Fraxinus excelsior)* and maple *(Acer pseudoplatanus)***

The growth parameters (growth rates, light demand of seedlings and saplings, tolerance to drought) were basically adapted from the forest landscape model LandClim (Schumacher and Bugmann 2006). Due to the calibration of LandClim to forest inventory data, tree species that are limited to wet sites by forestry tend to feature poor drought tolerance. This was the case for both, ash and maple. For ash, we set the drought tolerance to value slightly lower than beech and for maple a bit lower. Thereby, we achieved a realistic intermixing of hornbeam and ash in beech stands and the emergence of maple on the cool and wet North-facing slope of the valley. We kept the drought tolerance values of both below the ones of beech, because ash and maple retreat when beech and oak intermix in drier subcontinental climate.

**Calibration of evapotranspiration**

Following our approach in the Döberitzer Heide, we calibrated the potential (PET) and the actual evapotranspiration (AET) to observed values provided by the German Meterological Service (Deutscher Wetterdienst) for the period 1991 to 2014 (Figure 2). We used the average values among the two reference points in open landscape and forest and calibrated the PET to 545 mm per year and the AET to 417 mm per year.

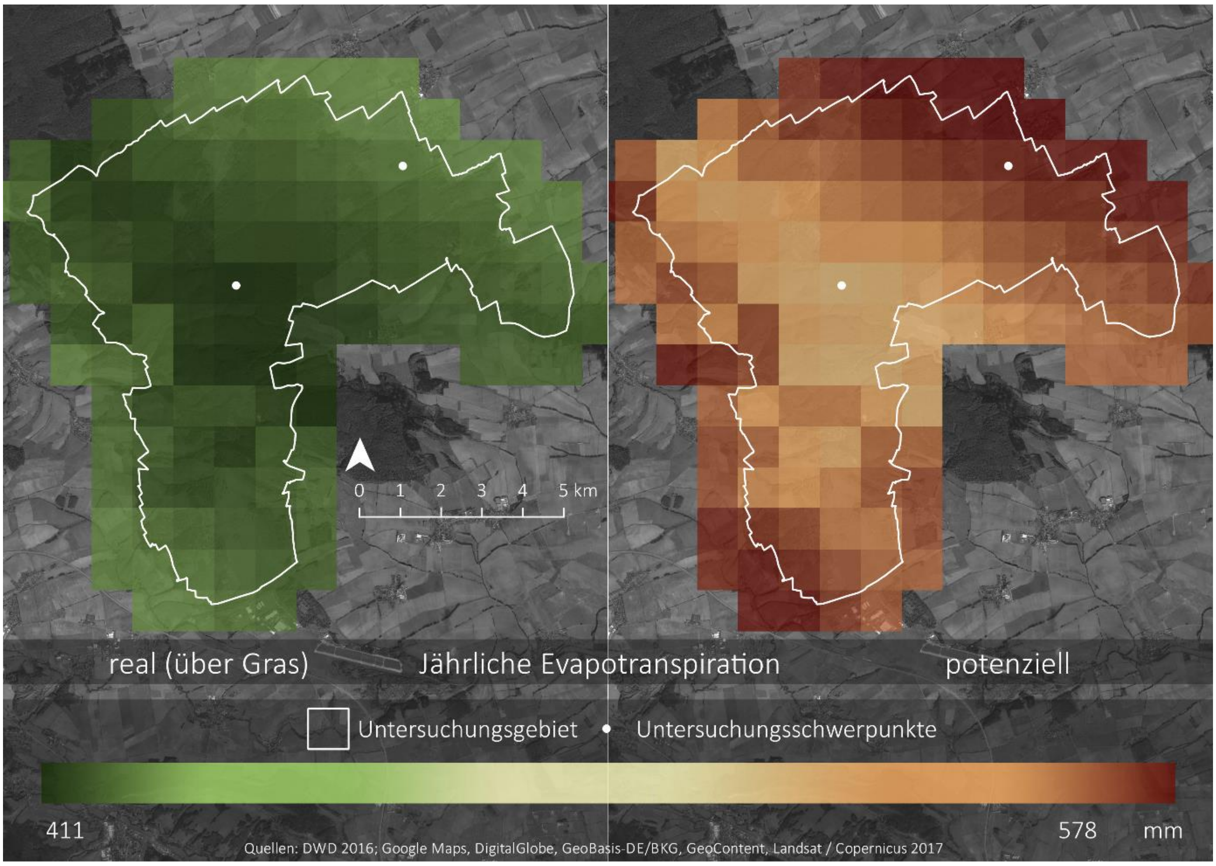



Figure 2 Maps of potential and actual evapotranspiration (real for grassland) according to the data of the German Meterological Service (Deutscher Wetterdienst). Aerial photograph: (DigitalGlobe, GeoBasis DE/BKG, GeoContent and Landsat/ Copernicus).

**Reproduction of the stand structure**

Regarding the stand structure, our spin-up simulations validated the total amount of seedlings in the understory, but did not reproduce the species diversity of tree regeneration. Huss and Butler-Manning (2006) mapped about 6 seedlings and saplings per meter square (3750 per 25 meters times 25 meters respectively), which fits well to our simulation of 3780 seedlings and saplings per grid cell of the same size. However, we simulated almost exclusively beech and only few regeneration of other species (Figure 3). To the contrary, observations showed a broad species diversity in some places, but in others not. The species diversity remained without explanation by the authors of the field survey and therefore may be a consequence of browsing or forest management history (refer to the review in Mölder et al. (2009). In turn, we did not calibrate on these patterns, but were satisfied to match the species-unspecific stand structure.

The dominance of beech in the understory supported the modelling of fast regeneration of beech stands after canopy gap-creation or disturbance, which is reported from beech forest in optimal growth conditions (structural analysis of virgin beech forests in Eastern Europe and of the Hainich). By this means, we may **overestimate the regeneration strength of beech stands** and may **underestimate their sensitivity to browsing and disturbance**.

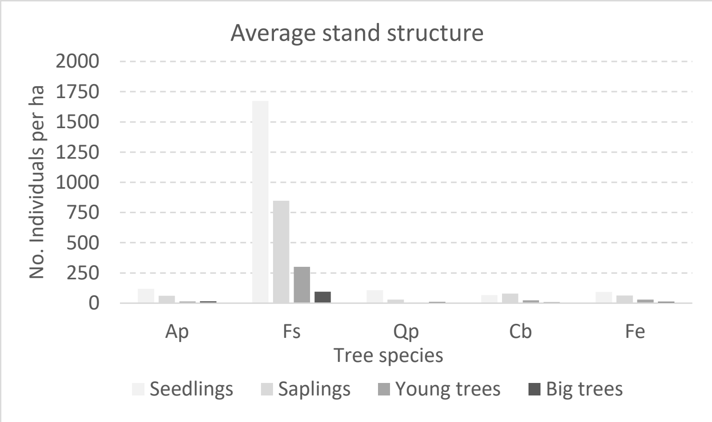



Figure 3 Mean stand structure of the forests in the artificial model landscape in the year 2015 AD (end of the spin-up simulation, start of scenario simulations). The y-axis shows the number of tree individuals in the four height classes of seedling (<30 cm), sapling (<1.5 m), young tree (<5m) and old tree (>5 m) for each tree species in the artificial model landscape. (Ap: maple, Fs: beech, Qp: oak, Cb: hornbeam, Fe: ash).

### 1.3.2 Calibration of herb layer vegetation types, succession and forage production

In previous model applications, the herb layer vegetation types represented the characteristic communities of subalpine pastures in the Swiss Jura Mountains, which are highly productive in suboceanic climate. For the model transfer to the Hainich, the simulated herb layer vegetation types were newly defined in terms of the characteristic plant communities of the Hainich. Their forage production in terms of quintals (decitonnes) per hectare and year was calibrated to agro-ecologic standard literature (refer to Table 3). These values were about three to five times as much as in the study area Döberitzer Heide, because of the rich substrate, comparatively high precipitation and long growing season. A high carrying capacity for herbivores resulted. Consequently, the same herbaceous forage demand of herbivores is expected to create and maintain smaller areas of open landscape by grazing.

Table 3 Plant communities and key species of simulated herb layer vegetation types (Ref.: Dierschke and Briemle 2008) and their forage production for grazing (Ref.: Dierschke and Briemle 2008; Nitsche and Nitsche 1994; Klapp 1965).

| Category | Plant communities and key species | Forage production |
|---|---|---|
| Productive grassland | **Arrhenatherum etiolaris / Mageres Lolio-Cynosuretum (Glatthaferweiden / Weidelgras-Kammgrasweiden):** *Arrhenatheretum elatius, Heracleum sphondylium, Dactylis glomerata, Alopecurus pratensis, Festuca pratensis, Holcus lanatus, Anthriscus sylvestris* | 50-80 dt/ha (ungedüngt) |
| Poor grassland | **Agrostis capillaris-Festuca rubra-community (Rotstraussgras-Rotschwingel-Gesellschaft):** *Agrostis capillaris, Festuca rubra, Deschampsia flexuosa* | 20-40 dt/ha |
| Fallow grassland | **Artemisietalia vulgaris / Galio-Convolvuletalia (Kletten-Beifuß-Staudenfluren / Klettenlabkraut-Zaunwinden-Saumgesellschaften)), Urtico-Aegopodietum (Brennnessel-Giersch-Flur)**: *Urtica dioica, Anthriscus sylvestris, Heracleum sphondylium, Rumex spec., Aegopodium podagraria, Dactylis glomerata, Lamium spec., Genista tinctoria, Vicia spec.* | 15 dt/ha |
| Understory | **Herblayer of Hordelymo-Fagetum/ Galio odorati-Fagetum (Waldgersten- bzw. Waldmeister-Buchenwald):** *Mercurialis perennis, Lathyrus vernus, Alium ursium, Hordelymus europaeus, Pulmonaria officinalis, Carex digitata, Carex muricata, Galium odoratum, Melica uniflora, Dentaria bulbifera, Asarum europaeum* | 5-10 dt/ha |

### 1.3.3 Modelling of browse spatial availability and digestibility

The modelling of browse entirely followed the approach established in the Döberitzer Heide.

### 1.3.4 Grazing and browsing patterns

The modelling of grazing and browsing behavior followed the approach established in the Döberitzer Heide. Again, distinct habitat use of separating herds was neglected. We simulated two herbivore scenarios: the common herbivore community consisting of red, roe and fallow deer, and a completed herbivore community including wisent. Abschlussbericht: Tabelle 7 gives the number of individuals and their forage consumption in terms of herbaceous forage and woody browse.

The **common herbivore community** had a low forage demand (4.3 kg DM) and a browsing preference (59%). Although red deer is considered to forage in an intermediate way (at least in absence of hunting), grazing and browsing patterns can be expected that are **similar to managed forests** (i.e. absence of glades but specific impact on tree species regeneration).

The **completed herbivore community** had a 1.5 times higher forage demand and a balanced diet. Nevertheless, their forage demand, especially regarding grazing, was well below the demand in the Döberitzer Heide. When considering the general higher forage availability in the Hainich (chapter 1.3.2), only **few forest glades** (due to low grazing pressure) and **a balanced habitat use among grassland and forest** can be expected in scenario simulations.

**Browsing plausibility check**

The spatial distribution of large herbivore habitat use of grazing and browsing result from the spatial distribution of herbaceous and woody forage at landscape scale (Chapter 1.3.2 und 1.3.3, forage chain) and topographic conditions in the artificial model landscape. Further, habitat use was related to repellent and attractive factors, in example, large herbivores avoid slope areas for means of low escape possibilities from predators or tree cover functions as a repellor for habitat use of grazing, thus the tree species-specific digestibility impacts habitat use of browsing.

Figure 4 shows the availability of herbaceous and woody forage in the artificial model landscape termed “forest edge” at time step 2015 AD. In the Figure, the spatial distribution of forage for grazing (“Herbaceous forage”) and browsing (“Digestible browse”) is shown. “Habitat use” indicates local high herbivore densities (individuals / ha year) for either browsing or grazing activity. Additional, Figure 4 shows in the column “utilization rates” the mean consumption rates of herbaceous and woody forage, which are indicators of local browsing and grazing pressure at patch scale. However, high browsing pressure is not an indicator of forage scarcity, but indicates patches of highly (digestible) attractive woody species (Chapter 1.3.3). Grazing and browsing pressure are the drivers of succession dynamics in the vegetation.

**The data-based parametrizations and developed processes of large herbivore habitat use, which were already applied to the “Döberitzer Heide”, also evoke plausible landscape patterns** in the artificial model landscapes representing limestone- beech forest as in the national park “Hainich” (Figure 4). Habitat use of grazing (column “habitat use”) mainly occurs in the open landscape areas Forage demand of the browser-dominated common herbivore community is however low (“utilization rate”). Therefore, grazing pressure in the open landscape is relatively low and fallow grasslands dominate. Further, grazing pressure is also too low in forest gaps that derive from natural tree mortality, because they are too small (25 m x 25 m) and are of low productivity.

Pattern of habitat use of browsing (column “habitat use”) shows that browsing activity is high in the forest, because of attractive “saplings” in the understorey, but also in the open landscape with attractive “shrub” and “saplings”. According to digestibility, beech is unattractive for browsers and therefore the amount of overall “digestible browse” is low in relation to the amount of available “browse”. As indicated by the utilization rates the overall browsing pressure is higher in open landscape areas, due to the overall scarcity of attractive (digestible).

According to the grazing and browsing patterns, they have in common that slopes are avoided for habitat use.

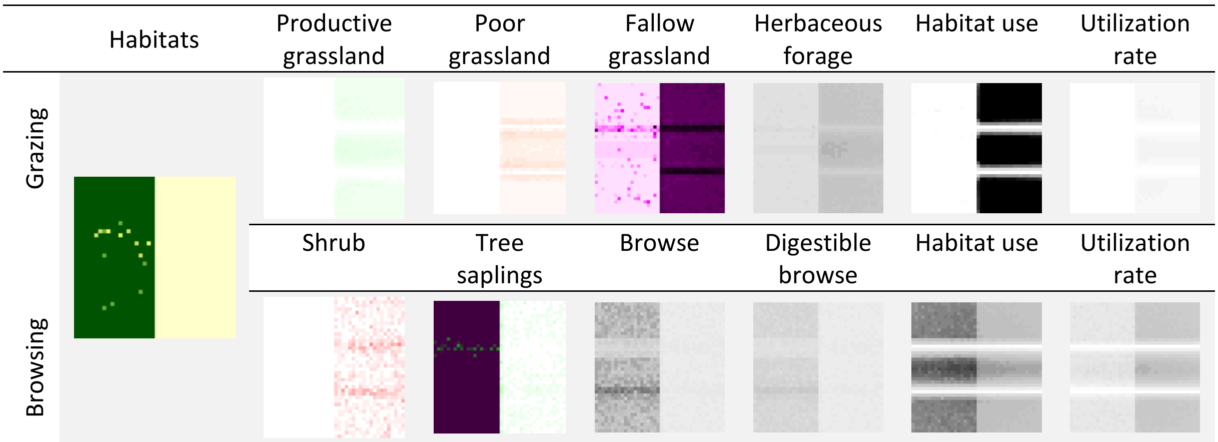



Figure 4 Availability of herbaceous and woody forage in the forest-edge landscape in simulation in year 2015 and its utilization for grazing and browsing by the common herbivore community. Herbaceous forage is expressed in kilograms dry matter per year and estimated from the herb layer vegetation types productive, poor and fallow grassland (refer to Table 3). Browse and digestible browse are expressed in kilograms dry matter per year and estimated from shrub and sapling cover. Darker tones indicate higher cover, more biomass or longer residence time per habitat.

The simulated grazing pattern is realistic, if hunting is inhibited. Then grazing activity of red and fallow deer naturally occurs in the open landscape (day active). Simulated low grazing pressure (10%) confirms our personal observations of the study site, of an open landscape with high standing biomass of fallow grasslands. As we simulate a low density, and both species have a relative low body weight, their grazing and trampling pressure alone are too low to disturb the dense fallow vegetation in the open landscape area. Also in the national park “Eifel” with higher deer densities, trampling is too low to open up the grass sward (S. Hudjetz, pers. comm.).

Simulated browsing pressure derives mainly from roe deer. Simulated habitat use of browsers results in plausible patterns, because roe deer prefer to forage on saplings and in the understorey in the forest, but also for reasons of shelter („thermal cover“). Browsing activity in the open landscape derives from simulated red and fallow deer. Both species are capable to inhibit tree establishment in the open landscape (Lennartz et al. 2009; S. Hudjetz pers. comm.). Therefore, the utilization rates in the open landscape for browsing are realistic, but only of 35%. In contrast to the observations in the „Eifel“, browsing pressure in the open landscape is too low to inhibit tree establishment / encroachment in the „Hainich“.

In simulations, habitat use of the common herbivore community in the “Hainich” is plausible. Regarding the complete herbivore community in scenario simulations including the wisent, the simulations of the “Döberitzer Heide” reveal plausible and realistic patterns. According to simulations in the „Hainich“ with the complete herbivore community, there is a decrease in beech cover due to increased browsing pressure. This is in line with observations from two wisent projects in Germany, in which beech has been heavily browsed by wisent (Damerower Wisentgehege, F. Zentner, pers. comm. and in the Rothaargebirge though low wisent density).

### 1.3.5 Initial clear cutting of forest

The modelling and simulation of the initial management practice of clear cutting is identical to the method in the Döberitzer Heide. The reproduced disturbance pattern was evaluated as highly realistic in an international review process (Peringer et al. 2017).

### 1.3.6 Wildfire ignition and spread in dense beech forest

The plant fuel load from the vegetation is high in dense beech forests due to a high abundance of saplings and undecomposed litter. However, because of its typical **fresh-humid forest climate**, in dense beech forests **wildfire ignition seems unlikely**. Wildfires can spread from the forest edges into the beech forest area, as it was observed in the Tessin. Here wildfires spread from the lower chestnut forest groves uphill into the beech forests (Maringer et al. 2016).

In order to simulate this effect on dense beech forests, we set a **threshold for wildfire ignition regarding the maximum tree cover**. This threshold was set at 70% tree cover. In accordance to the phytosociological analysis of Gallandat et al. (1995), forests with a tree cover of equal or more than 70% tree cover inhabit species that depend on a forest climate. Wildfire spread into neighboring grid cells is not affected from this threshold, and spread only depends on the local fuel load in each grid cell. In the simulation study, “Döberitzer Heide” we did not regard this threshold for maximum tree cover. Here, canopy cover of oak, hornbeam and pine is far more sparsely and forest climate is not as relevant.

Identical to the simulation study “Döberitzer Heide”, the simulated wildfire ignition depends on the combined factors of monthly aridity (threshold of 30) and the fuel load (biomass) from the woody vegetation and cover of fallow grasslands.

**Wildfire ignition and spread plausibility check**

In the forest scenarios, it was most obvious that the dense cover of beech **inhibited wildfire ignition although there was plenty of fuel and prevailing drought stress**. Only in **forest gaps** and in **thinned out forest patches** (herbivore-effect, drought stress) **on shallow soil**, wildfire ignition was possible. In burned patches tree mortality increased and the stand structure was modified, therefore these burned patches had an increased fire proneness in the succeeding decades (refers to the fire-fire-feedback, Hobbs 2006).

The ignition of isolated small wildfires in gaps depends on the above factors. These isolated wildfires then slowly spread into the neighboring patches. Especially in forest patches thinned out by large herbivore habitat use for browsing wildfire spread is high. Habitat use of grazing can induce so called "fuel breaks" (Hobbs 2006). Grazing decreases spatial fuel loads, and especially in grazing lawns, wildfires cannot spread because the grass sward is too short. However, in our simulations, the herbivore density might be too low to evoke this herbivore-fire-effect.

Figure 5 summarizes the simulated effects on beech forest in the artificial model landscape "forest" in the wildfire years 2025 AD, 2065 AD and 2069 AD. The Scenario 3.5, "Common herbivore community and wildfire" was simulated. From initial closed forest, both the number of burned and of fire prone patches spread and slowly increase over time. This development corresponds to the fire-fire-feedback (Hobbs 2006), burned gaps increase towards burned areas. The simulated burned areas are only of small size with a diameter of 50 to 75 m (two to three grid cells). In comparison to the burned areas in the Tessin (pers. observation, Maringer et al. 2016), the **potential of simulated wildfire spread might be underestimated**.

The simulated effects on the herb layer in terms of temporal biomass increase (forage productivity) in burned patches and therefore increased habitat use of grazing in burned patches (e.g. Scenario 1.6, 2130 AD in Figure 12 and Figure 15) correspond to those already presented and plausibility-checked in the study "Döberitzer Heide".

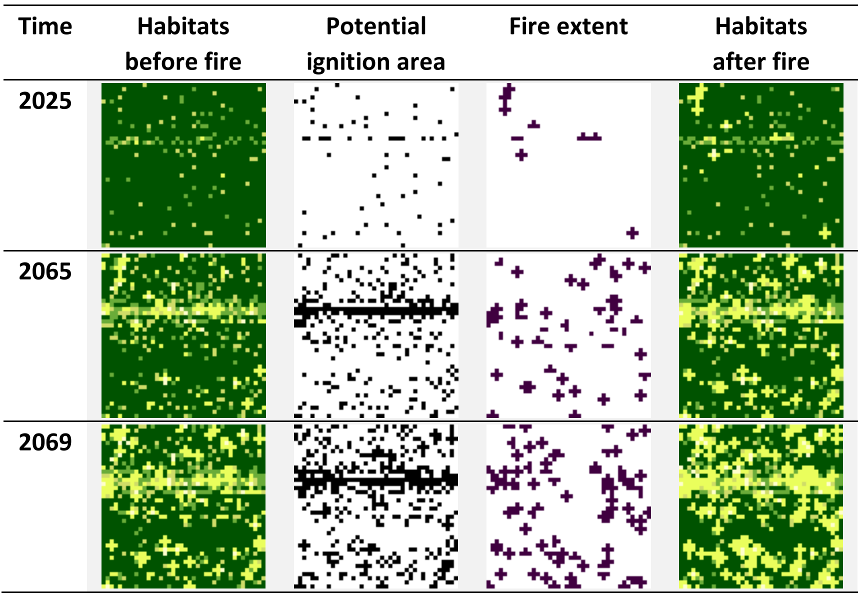



Figure 5 Simulated wildfires in initially dense beech forest in years 2025, 2065 and 2069 AD (drought for fire ignition is based on the local specific climate time series for the Hainich and therefore differs from the Döberitzer Heide ignition time series). The maps show the habitat distribution before fire, the potential ignition area based on the availability of fuel and tree cover being below 70%, the simulated fire extent with a 15% probability of each grid cell to be ignited and the habitats after the fire. We show habitats instead of tree cover, because fire ignition is suppressed in the forest habitat type (darkest green), but not in the other habitats (lighter green tones, for habitats refer to Table 2 and to Figure 12 for a color legend). Thus, the increase in potential ignition area is clearly indicated. The maps demonstrate the fire-vegetation-feedback saying that once burned area is more susceptible to fire in the near future.

### 1.3.7 Stochastic woody plant establishment from long-distance dispersal

For the colonization of open land by woody species, scattered outpost-tree colonization is important. Early successional patterns depend on this process, although the general establishment probability in a single year is low (long-term observations of Peringer and Rosenthal on *Alnus glutinosa* establishment on extensively grazed fens). The modeling of outpost-tree colonization in the grasslands of the Hainich followed the stochastic approach that was developed in the Döberitzer Heide.

**Woody plant establishment plausibility check**

We simulated the abandonment succession on grasslands of the Hainich National Park, which were cleared from forest in the early 1980ies and only partly grazed by livestock afterwards (Wikipidia, 24.4.2017) and compared the simulated patterns to observed ones. We started our simulations from the open landscape state and simulated 35 years of succession under the presence of the common herbivore community until 2015. The simulated patterns of early woody plant encroachment resulted from long-distance dispersal only, because no trees were present at the start of simulations and 35 years is too short for most tree species to reach maturity.

Figure 6 shows plausible results when compared to aerial photographs and field observations (Figure 7). Shrubs, poplar and birch ran early woody plant succession and only few grid cells were colonized by maple, hornbeam and oak (Figure 6). Tree species established in higher cover at the valley slopes that are avoided by herbivores, indicating the role of the common herbivore community in controlling woody plant succession. Oak and maple were restricted to these sites, where also dense shrub cover provided shelter from browsing. Birch, poplar and shrubs also colonized the surrounding plains with a scattered mosaic pattern.

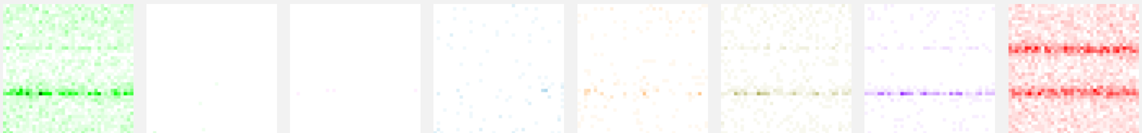
| Tree cover | Beech | Hornbeam | Oak | Maple | Birch | Poplar | Shrub |
|---|---|---|---|---|---|---|---|
|  | | | | | | | |
| 0.8% | 0.003 % | 0.02% | 0.06% | 0.08% | 0.25% | 0.24% | 9.0% |

Figure 6 Spatial distribution of tree species and shrub in the open landscape scenario after 35 years of abandonment succession (starting in calendar year 1980, ending in 2015) and the common herbivore community. Tree species maps show the cover times 10 (color range covers 0 - 10% instead of 0 -100% of the maps in the appendix, Figure 15). The map for shrub cover show 1-100% cover.


Figure 7 Scattered outpost-tree colonization patterns and establishment along linear nurse structures (from North to South) on the grasslands at the parking place “Zollgarten” in the Hainich National Park (Aerial photograph: (DigitalGlobe, GeoBasis DE/BKG, GeoContent and Landsat/ Copernicus), patterns verified in personal field observation).

This development **was related to the observed patterns** in the Northern open landscape area of the Hainich National Park (Figure 7 and personal observations during a field survey guided by J. Wilhelm). Here, scattered widespread outpost-tree colonization by ash and oak dominates and is facilitated by nurse shrubs (*Prunus spinosa, Crataegus spec*). The habitus of tree and shrub showed browsing damage by wild herbivores. In our simulations, birch and poplar took this early colonizing role and their facilitation along the valley slope matched the observed herbivore impact (Figure 6). Along nurse structures, thickets developed (Figure 7), which corresponded well to the more dense shrub and tree cover at the valley slopes in our simulations (Figure 6).

Beech failed to establish in the open landscape and did so in our simulations. Beech obviously requires the shelter of thickets to establish, which is slow because of the dense grass sward on rich calcareous soil (loess). To the contrary, on cleared forest sites, dense stands of young hazel, elm, *Crataegus*, ash, poplar and maple developed within 25 years and today beech establishes here. We did not test such disturbance effects for plausibility check, but the regeneration after initial clear-cut in scenario 3.3 showed a plausible development of medium wooded habitats within a decade and ongoing densification towards densely wooded habitats afterwards (Figure 8).

Altogether, the model **reproduced the main colonization patterns well in terms of structure** (scattered outpost-trees and thickets along nurse structures), but **only partly in terms of tree species composition**. Outpost-trees were simulated as birch, poplar, maple, hornbeam and oak, but only ash and oak were observed. As fast-growing early-successional birch and poplar was simulated but lacks in reality, our model might **overestimate the speed of forest development** and **underestimate the persistence of open land**.

### 1.3.8 Tree and shrub mortality from natural decay

The mortality of old trees is a key process during the adaptation of forest communities to climate change (recent work of the Bugmann-group at ETHZ). Put into the context of regressive succession driven by large herbivores, forest gaps are preferentially grazed and tree regeneration browsed. Therefore, the die-off of old trees conditions the future structure of semi-open landscapes, when gaps are enlarged to glades by herbivore pressure.

The decay of shrubs (heather and broom) provides windows of opportunity for the establishment of light demanding pioneer species inside thickets of old branches. Here saplings are protected from Browser and do not suffer from resource competition with the shrub itself.

The factors that drive the mortality of tree and shrub are hard to estimate from environmental conditions such as drought. The resulting die-off is often delayed for years to the occurrence of stressors and is often the consequence of the cumulative influence of several factors, e.g. insect attacks on trees weakened by drought. We therefore modelled tree and shrub mortality as a stochastic process related to the approximated maximum age of the dominant late successional tree species (200 to 250 years for *Fagus sylvatica*) and of shrubs (about 50 years for *Prunus spinosa* and *Crataegus spec.*). The low maximum age of beech was specifically adapted regarding the well growth conditions in the Hainich, where beech grows fast and early suffers from crowns becoming too large to stand windstorms (J. Wilhelm, pers. communication). Huss and Butler-Manning (2006) estimated an age of 200-250 years of recently collapsed beech.

**Modelling of tree and shrub mortality**

For trees, we simulated a yearly creation of gaps in the forest canopy by the breakdown of senile trees in 0.5% of the landscape (number of grid cells respectively), which results in an average return interval of 200 years for an old tree to collapse. Following the approach established in previous studies, the gaps were stochastically distributed and the topmost tree layer was cleared. A similar proportion of gaps was observed for virgin beech forests in Eastern Europe (Schliemann and Bockheim 2011; Zeibig et al. 2005).

For shrubs, we simulated a yearly die-off in 2% of the landscape (number of cells respectively). The mortality was also stochastically distributed and had an average return interval of 50 years. Following a mortality event, only 50% shrub cover was removed in order to consider a partial vegetative rejuvenation of large shrub individuals.

**Tree and shrub mortality plausibility check**

Stochastic tree mortality led to a realistic distribution of gaps in the forest canopy that were in different stages of gap closure at the end of the spin-up simulation (refer to the distinct tones of green in the habitat map in Figure 4; in sum 3% of the grid cells had less than 70% tree cover).

For shrub mortality, we had no reference pattern at hand. Moreover, shrub decay during the course of succession was driven by light competition with pioneer trees and therefore followed their establishment pattern.

## 2 Results in detail

### 2.1 Arrangement of trajectories and maps

From the plenty of model output we elaborated maps of the state variables of vegetation and plotted trajectories of these state variables after aggregation over the entire landscape. We complemented the maps and trajectories with a set of derivative variables that are important to understand the emergence of certain patterns, such as the spatial habitat use of herbivores for progressive and regressive vegetation succession, the spatial distribution of habitat types derived from tree cover and an index that captures landscape structural heterogeneity. Table 4 allocates the variables to the figures.

Table 4 Figures that show maps and trajectories for state variables and derivatives. The habitat types are defined in Table 2.

| Variable | Map | Trajectory |
|---|---|---|
| Tree species cover | Figure 15 | Figure 10 |
| Herb layer vegetation types cover | Figure 14 | Figure 11 |
| Habitat types | Figure 12 | Figure 8 |
| Landscape aggregation index | - | Figure 8 |
| Habitat use of herbivores | Figure 13 | - |

The trajectories of habitat development (relative cover of habitat types as defined in Table 2) and of landscape-structural diversity are shown first for their overview to successional patterns, i.e. periods of progressive or regressive succession, fluctuations, disturbance impacts and the development of habitat mosaics. The trajectories of tree species cover are shown second, because the spatial population dynamics of tree species explain landscape structural change. The trajectories of the cover of vegetation types in herb layer are shown third for their indication of the nature conservation value of open landscape habitats. All figures with trajectories are arranged to compare disturbance scenarios in rows and the herbivore scenarios in columns.

We show maps on the composition of the herb and tree layer.

### 2.2 Landscape development under common herbivore community

In simulations only with the **common herbivore community in the open landscape scenario** (Scenario 1.1), initial open landscape encroached moderately due to progressive succession of fallow grassland and shrub until 2150 AD (Figure 8). From then onwards, progressive tree succession increased and sparsely wooded habitats of pioneer species (birch, poplar, pine) densified into medium to densely wooded habitats (oaks, hornbeam and beech; Figure 8, Figure 12 and Figure 15).

Forest development (until 2200 AD) in initial open landscape takes so long because of the initial dense cover of fallow grassland and the low grazing pressure of the common herbivore community (Figure 10 and Figure 14). For decades, the dense grass sward inhibits dispersed tree species to establish. Although open landscape is at a state of moderate stability, because woody encroachment is slow, it cannot provide habitat requirements for certain species of the open landscape. In the last years, woody encroachment was observed in the "Hainich". Due to its short time since abandonment, there was an availability of gaps in the open landscape and long-distance dispersed tree species had an opportunity to establish. As indicated in Figure 7, by the linear colonization pattern of woody species in the open landscape. Currently, fallow grassland dominates and scattered isolated trees occur without a developed stand structure.

In simulations only with the **common herbivore community in the forest scenario** (Scenario 3.1), dense forest cover was maintained in the long-term. Only for short periods, climate change induced drought stress lead to thinning out of the dense beech cover, especially on edaphically dry and shallow soils at the south-facing slope (Figure 8 and Figure 12). Climate change-induced drought stress decreased beech cover to the profit of hornbeam and oak (Figure 10 and Figure 15), but in the long-term beech dominated. Light-demanding tree species only increased at the south-facing slope.

In simulations with the **common herbivore community and initial clear cutting in the forest scenario** (Scenario 3.3), only for about one decade the combined effect of foraging pressure and clear cutting evoked unwooded and sparsely wooded habitats (Figure 8). Forest thinning caused by climate change-induced drought stress was higher and this facilitated an increased establishment of oak (Figure 10, Figure 12 and Figure 15). However, the long-term landscape pattern and forest community referred to the simulation of the undisturbed forest landscape scenario (compare to Scenario 3.1, Figure 12).

In simulations with the **common herbivore community and wildfire in the forest scenario** (Scenario 3.5), already from the first wildfire event on in 2025 AD forest gaps developed in burned forest patches (Figure 12). In burned patches **in the open landscape** (Scenario 1.5), progressive succession of pioneer tree species was delayed (Figure 10 and Figure 15) and wildfires facilitated dry grasslands in burned patches (Figure 11 and Figure 14). Even under the low density of common herbivore community, wildfire-effect on landscape openness lasted for decades. However, landscapes patterns developed into dense forest cover in the long-term (Figure 8 and Figure 12). Large herbivore grazing pressure was too low to maintain patches of poor grasslands continuously and they did not provide the habitat requirements for open landscape species (Figure 14).

In the **open landscape and forest scenarios, simulated wildfires modified** the forest **structures** and **communities of forests and shrubs** sustainably. Beech lost in dominance to the profit of fire-tolerant oak and further light-demanding tree species (Scenario 3.5, Figure 10). Landscape developed a structurally rich mosaic with stands of birch, poplar, pine and oak (Figure 15). Pine dominated at the edaphic dry and wildfire prone south-facing slope (compare potential wildfire ignition areas in the years 2065 and 2069 AD in Figure 15). Beech remained dominant in the fresh-moist climate at the north-facing slope, where wildfire occurrence was rare (compare potential wildfire ignition area in the years 2065 and 2069 in Figure 5). Additional, at the north-facing slope, water soil conditions are favorable for beech regeneration. Wildfire had a stabilizing effect on the shrub community in the open landscape (Scenario 1.5), because wildfires destroyed cover of and weakened saplings of pioneer species (Figure 10). Forest fires (Scenario 3.5) evoked patches of early-successional shrub species and grassland (compare 2100 and 2200 AD, Figure 11). These burned forest patches had an increased potential for wildfire ignition (fire-fire-feedback, Hobbs 2006) to the profit of grassland species. Nevertheless, due to their highly scattered pattern, colonization and migration among isolated burned patches of open landscape species was difficult.

In simulations of the **forest scenario with the common herbivore community combined with initial clear cutting and wildfire** (Scenario 3.7), from initial forest area large patches of open landscape were generated until 2100 AD (Figure 12), but in the long-term open landscape was lost. Until 2200 AD, beech dominance decreased and thin canopy mixed oak forest stabilized (Figure 10). Simulated initial clear cutting in the forest scenario (Scenario 3.3) thinned out dense beech canopy and because this destroyed the fresh-humid forest climate, the potential for wildfire ignition within beech forest increased (see 2030 AD, Figure 12). Generally, clear cutting increased the amount of potential wildfire ignition areas (compare Scenarios 3.5 and 3.7 in 2030 AD, Figure 12). This increase of burned patches facilitated the long-term opening of beech forest and shifted tree species diversity in the forest. In simulations of the forest scenario with the common herbivore community combined with initial clear cutting and wildfire (Scenario 3.7), from initial forest area large patches of open landscape were generated until 2100 AD (Figure 12). Until 2200 AD, beech dominance decreased and thin canopy mixed oak forest stabilized (Figure 10). Simulated initial clear cutting in the forest scenario (Scenario 3.3) thinned out dense beech canopy and because this destroyed the fresh-humid forest climate, the potential for wildfire ignition within beech forest increased (see 2030 AD, Figure 12). Generally, clear cutting increased the amount of potential wildfire ignition areas. This increase facilitated the long-term opening of beech forest and shifted tree species diversity in the forest. Low grazing pressure in the generated large open patches is not high enough to inhibit progressive fallow grassland succession (Scenario 3.7, Figure 11). Until 2200 AD, the vegetation adapted to a wildfire disturbance towards a fire-tolerant forest community. Long-term landscape pattern was similar to that in the forest scenario only with a wildfire regime (compare 3.5 and 3.7, Figure 8 and figure 12).

**Altogether, the simulations in the open landscape and forest scenario** with the common herbivore community showed that **habitat use of the common herbivore community could not maintain open landscape sustainably and not generate semi-open habitats from current forest**. Even not at sites, at which climate change-induced drought stress decreased dominant beech cover (south-facing slope). Also in combination with initial clear cutting, in the log-term open landscape was lost. Therefore, the habitat type of semi-natural dry grasslands and scrubland on calcareous substrates (Natura code (*) 6210) is threatened. Further one can expect the development of orchid lime beech forests (Natura code 9150) in current Asperulo-Fagetum beech forest (Natura code 9130).

From all scenario simulations, simulated **wildfire regime had the strongest landscape-engineering effect in that it generated open patches in initial forest in the mid-term and slowed down progressive succession in the open landscape.** Burned patches in the forest and in the open landscape represented habitats for early successional species. However, habitat requirements for light-demanding open landscape species in poor and productive grasslands were low in these burned patches due to the low grazing pressure. Habitat requirements and habitat continuity in open habitats were of low quality because of rapid progressive tree and fallow succession in between wildfire events. Again, the habitat type of semi-natural dry grasslands and scrubland on calcareous substrates (Natura code (*) 6210) is threatened. Regarding the low fire-tolerance of beech forest, one can expect the expansion of thermophile oak forest (Natura code 9170) and increase of fire-tolerant oak-pine-forests.

### 2.3 Landscape development under completed herbivore community

In the **open landscape and forest scenarios only with the completed herbivore community** (Scenario 1.2 and 3.2), habitat use had the potential to **maintain unwooded habitats at small-scale and evoke sparsely wooded habitats** (Figure 8 and Figure 12).

In **open landscape scenario with completed herbivore community** (Scenario 1.2), the additional **foraging pressure of wisent** slowed down progressive tree succession in the open landscape and maintained sparsely wooded habitats for several decades (Figure 8). To the majority, browsing pressure inhibited the establishment of pioneer birch and poplar and less of shrubs (Figure 10 and Figure 15). Therefore, structures for complex habitat species stabilized for a long time of period (red-backed shrike, *Lanius collurio*). From about 2150 AD onwards, successful tree establishment of pioneer species decreased landscape openness and browsing-effect on openness was limited to small patches within the main foraging sites (in vicinity to the watering point, Figure 8). At first, these small patches appeared segregated from the forest area, as it is common for wooded pastures. However, over the long-term grazing pressure induced the emergence of a continuous area of poor and productive grassland (Scenario 1.2, Figure 13 and Figure 14).

Generally, in the open landscape and forest scenarios with complete herbivore community (Scenarios 1.2 and 3.2), the high grazing pressure increased the overall amount of grassland communities that are typical for extensive grassland systems (Figure 11 and Figure 14). In comparison to Scnearios with the common herbivore community (compare to Scenarios 1.1 and 3.1), open patches in the open landscape were dispersed in a more continuous pattern and the number of open patches in the forest was higher (Figure 12). Nevertheless, at the simulated herbivore density, grazing pressure was too low to weaken the dominance of fallow grassland (Figure 14). To increase the foraging pressure in the open landscape a further complementation with a grazer species, as the Przewalski-horse, could be advantageous (as shown in simulation of the Döberitzer Heide).

Due to the intermediate habitat use of wisent, habitat use of browsing was higher in simulations of the completed herbivore community. In comparison to simulations with the common herbivore community, browsing pressure was up to 30% higher. In the **forest scenario** (Scenario 3.2), already to the mid-term, **enhanced browsing pressure facilitated the emergence and maintenance of semi-open habitats, modified the tree cover and tree diversity**. Thus, overall cover of sparsely to medium wooded habitats was higher than that of dense forest (Figure 8 and Figure 12). Regarding habitat diversity in forest scenarios with completed herbivore community (Scenario 3.2), there was a higher diversity and at spatio-temporal scales habitats occurred more evenly, for example maintenance of unwooded habitats at about 10% until the end of the century (2100 AD, Figure 8). According to the landscape aggregation index that indicates landscape complexity, herbivore habitat use of the completed community facilitated the generation of landscape mosaics of high structural complexity (Figure 8).

In the **forest scenario** (Scenario 3.2), **selective browsing behavior** of the completed herbivore community in combination with climate change-induced drought stress thinned out beech forest from 2015 AD onwards (Figure 8). Browsing **reduced the competitive strength of beech and attractive hornbeam to oak and the light-demanding species** birch, poplar and pine; however, beech remained the dominant species within existing forest stands (Figure 10 and Figure 12).

Browsing pressure in existing forest stands generated habitat requirements for light-demanding tree species, and in the open landscape scenario (Scenario 1.2) browsing pressure on light-demanding species was very strong (Figure 10). Cover of oak temporally increased due to high browsing pressure and developed a uniform spatial distribution (Figure 15). Oak distribution enhanced habitat connectivity for species bound to old oak tree (in the sense of habitat trees).

In simulation of the **forest scenario with completed herbivore community and initial clear cutting** (Scenario 3.4), clear cutting generated sparsely wooded habitats only for one decade (Figure 8), forest thinning driven by climate change-induced drought stress and oak establishment enhanced (Figure 10 and Figure 12). Successional transition phases of medium wooded habitats lasted longer (2150 AD, Figure 8) due to the increased browsing pressure of the completed herbivore community. Also densely wooded habitats in thinned out forest lasted longer, until 2250 AD (Figure 8). Under the completed herbivore community, effects of initial clear cutting last longer.

In simulations of the **forest scenario with the completed herbivore community and wildfire** (Scenario 3.6), the combined effect of habitat use and wildfire **positively influenced the emergence and maintenance of landscape openness**. From 2050 AD on, during regular wildfire events unwooded to sparsely wooded habitats emerged at large scale and persisted in the long-term (Figure 8). Although foraging pressure was high in burned patches and slowed down post-fire tree regeneration, foraging pressure was not high enough to develop fuel breaks (herbivore-fire-vegetation feedback, Hobbs 2006, as in simulations of the Döberitzer Heide). Therefore, simulated wildfire spread and wildfire extent were high. Fire-tolerant oak increased in cover on the cost of fire-intolerant beech (Figure 10), beech stands only maintained on the less fire prone north-facing slope (Figure 15).

As well in the open landscape and the forest scenario (Scenarios 1.6 and 3.6), wildfires evoked continuous open patches at large scale, in these open patches habitat use of grazing maintained poor and productive grasslands (Figure 11). Therefore, the combined impact of wildfire and grazing pressure facilitated habitat connectivity and spatio-temporal continuity for open landscape species (Figure 14).

In the **forest edge scenario with wildfire** (Scenario 2.6), the **initial segregated landscape pattern dissolved** due to the impact of regular wildfire events until 2200 AD (forest edge, Figure 12). However, habitat use of grazing remained higher in the initial open landscape with productive grasslands on deep soils and was too low in the disturbed forest edge area (Figure 13 and Figure 14). Therefore, after 2200 AD when wildfires became fewer, the segregated landscape pattern returned.

In simulations of the **forest scenario with the completed herbivore community, wildfire and initial clear cutting** (Scenario 3.8), the **positive effects on landscape pattern and dynamics induced by initial clear cutting enhanced**. In these simulations, already early initial clear cutting generated large open patches of unwooded to sparsely wooded habitats, which facilitated wildfire spread among the landscape. Additional grazing pressure by the completed herbivore community in burned areas stabilized landscape openness (Figure 8). Already at the end of this Century, beech was lost at the higher levels (Figure 10). Until 2150 AD, semi- to open habitats remained at a stabile state and provided habitat requirements for species of poor and productive grasslands (Figure 14). From then on, cover of oak increased in open landscape areas.

Altogether, simulations with the **completed herbivore community showed that their habitat use increased habitat qualities for species of the open landscape and forest**. **In relation to habitat continuity, spatial connectivity and extent**, for as well species of poor and productive grasslands, and for the biodiversity linked to oak (habitat trees). Regarding the habitat type of semi-natural dry grasslands and scrubland on calcareous substrates (Natura code (*) 6210), simulations indicated a moderate conservation status. Furthermore, the intermediate habitat use of the completed herbivore community facilitated the dissolvent of segregated landscape patterns (legacy effects). Intermediate foraging pressure had an integrated impact on the vegetation: browsing pressure thinned out beech forest and grazing pressure stabilized poor and productive grasslands.

Although, simulated browsing pressure of the completed herbivore community was higher than that of the common herbivore community, in simulations without wildfire beech remained dominant. Thus, novel oak stands established. Regarding the habitat type of orchid lime beech forests (Natura code 9150), their cover should increase in thinned out forest canopy and towards the transition to thermophile oak forests (Natura code 9170).

Though simulated low herbivore density, the **completed herbivore community maintained unwooded and sparsely wooded habitats in open areas generated from initial clear cutting and wildfires**, in the long-term. To the mid-term, landscapes provided potential large areas for the habitat type of semi-natural dry grasslands and scrubland on calcareous substrates (Natura code (*) 6210). Thermophile oak forests (Natura code 9170) and fire-resistant oak-pine-forests replaced beech stands. Further, orchid lime beech forest (Natura code 9150) was lost in these simulations.

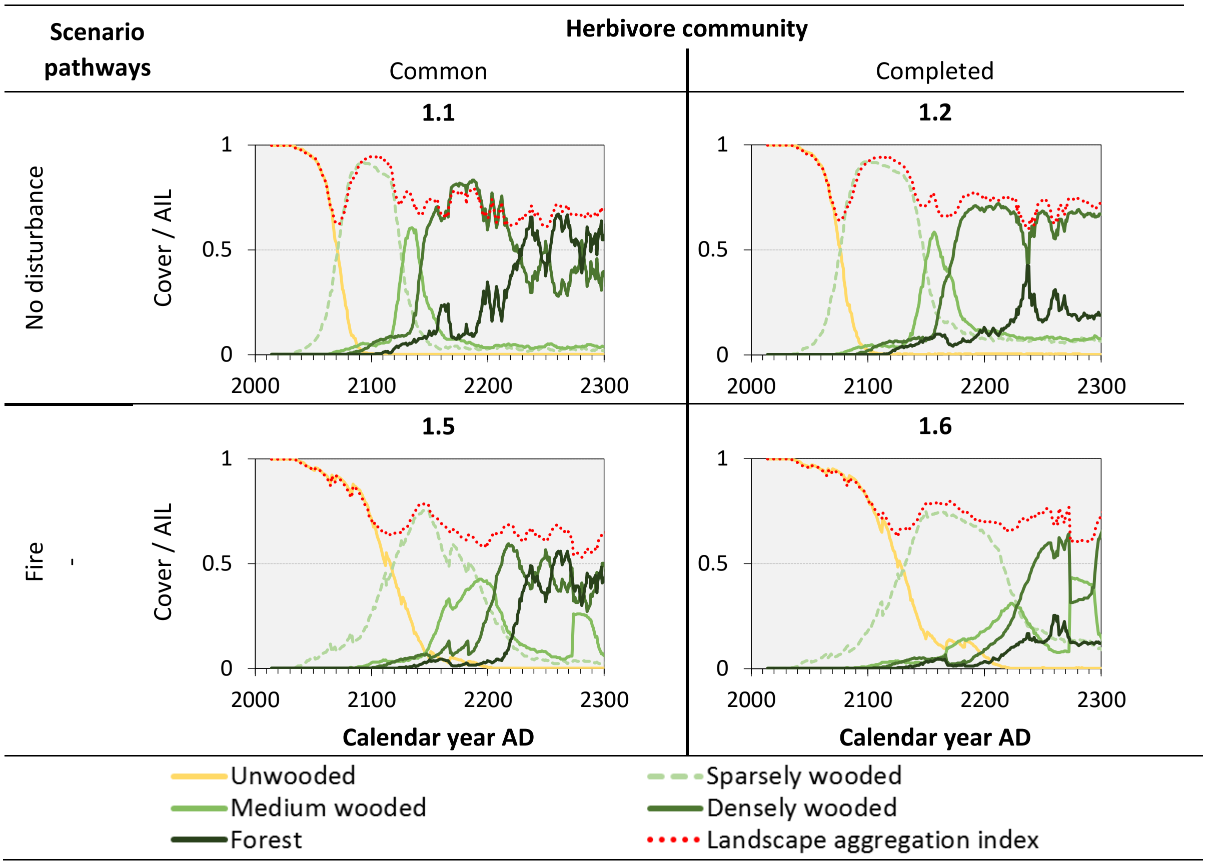



Figure 8 (including the following two pages) Trajectories of the relative cover of habitat types (defined in Table 2) and landscape-structural diversity (indicated by the landscape aggregation index AIL) for all scenarios, this page: **open landscape scenario**. Index values of AIL towards zero indicate landscape disaggregation and heterogeneity, whereas values towards one indicate simply structured aggregated patterns. In this figure, the **open landscape** scenario pathways are shown.

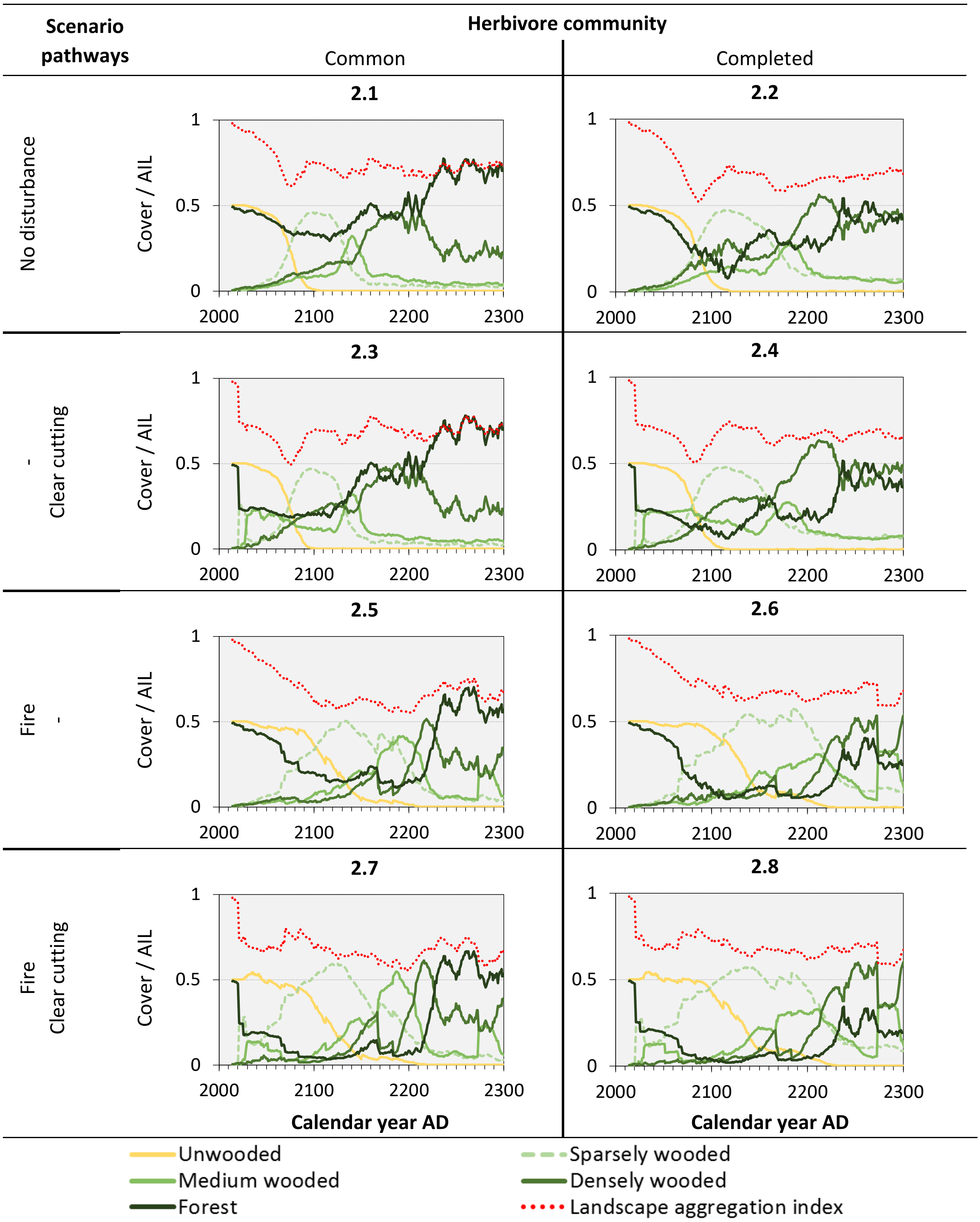



Figure 8-continued **Forest-edge scenario**

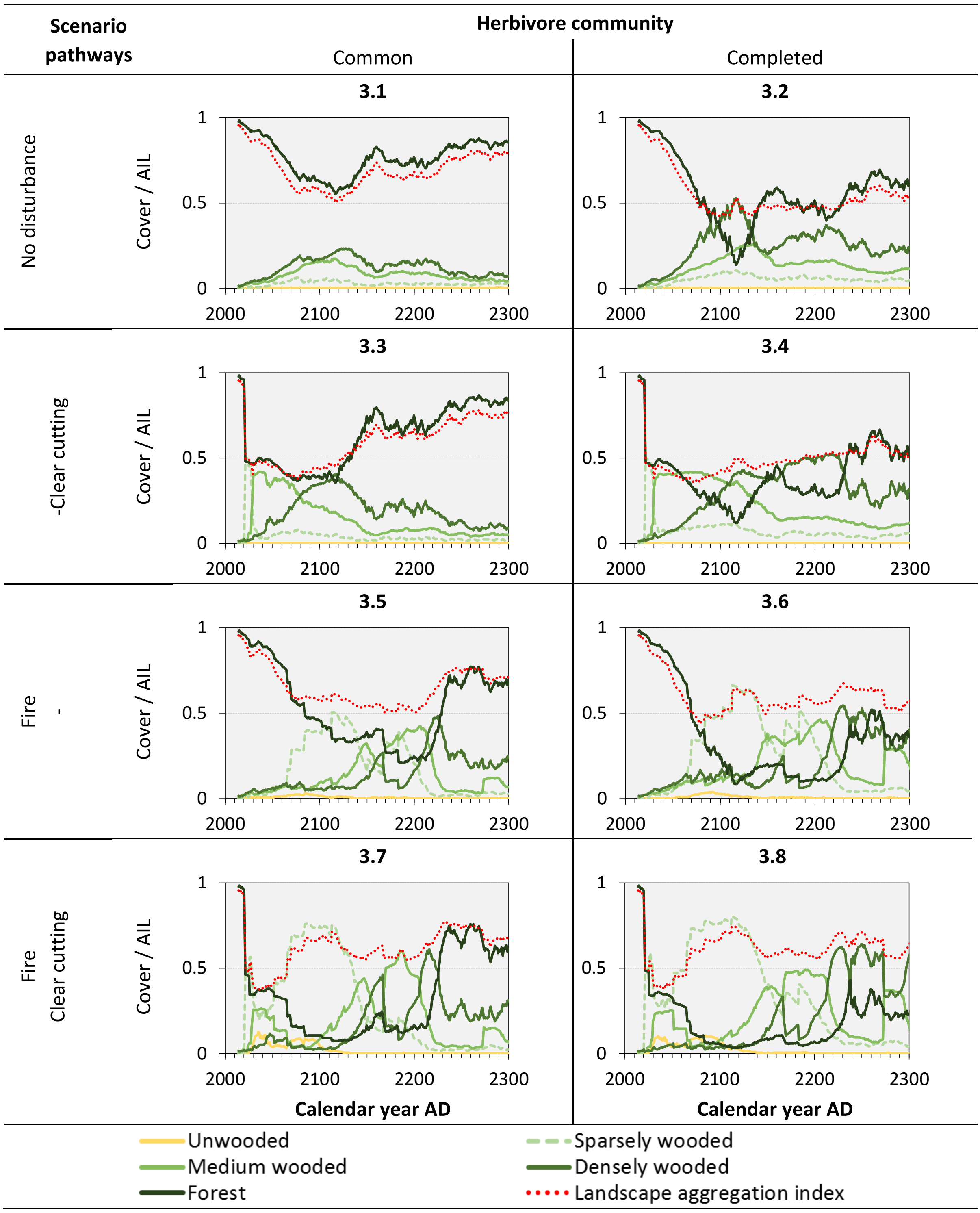



Figure 8-continued **Forest scenario**

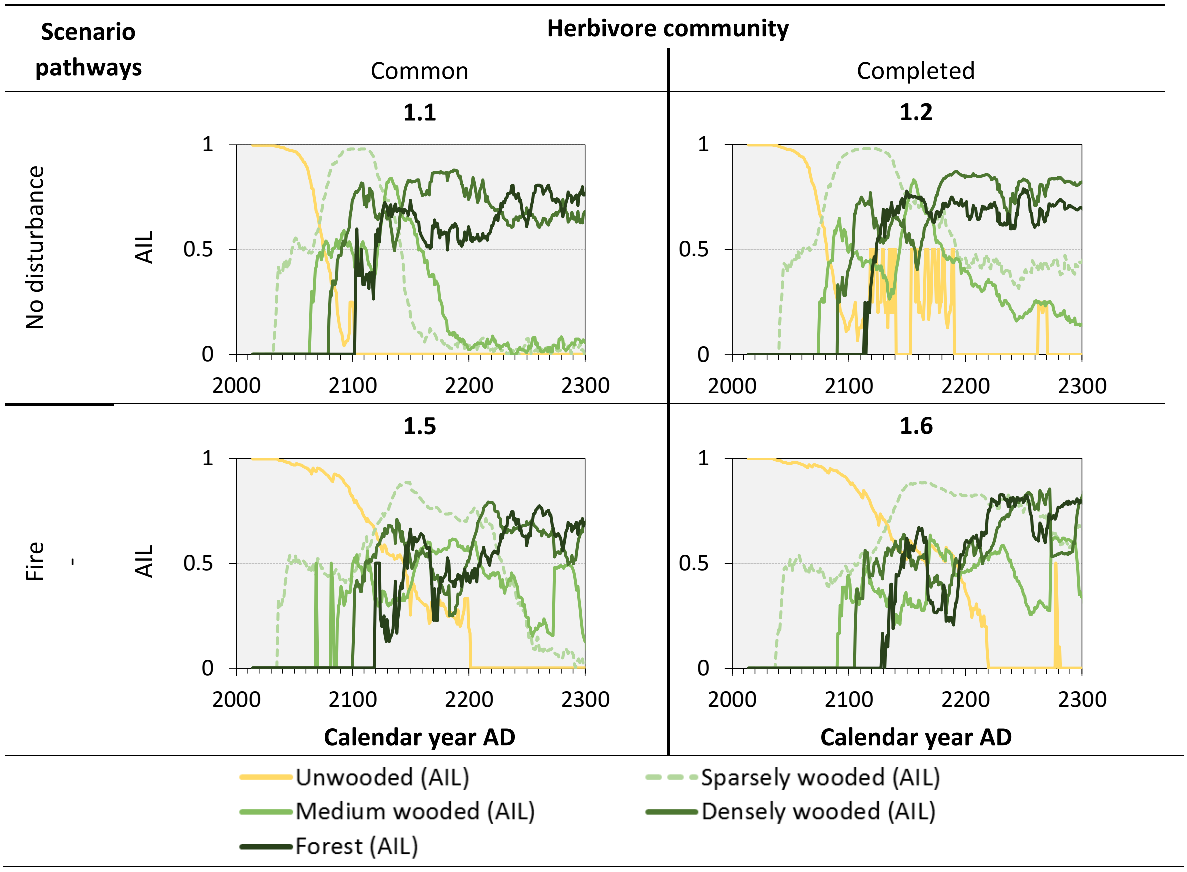



Figure 9 (including the following two pages) Trajectories of the landscape aggregation index (AIL) specific for the habitat types for all scenarios. Index values of AIL towards zero indicate habitat disaggregation and heterogeneous distribution, whereas values towards one indicate simply structured aggregated patterns. In this figure, the **open landscape** scenario pathways are shown.

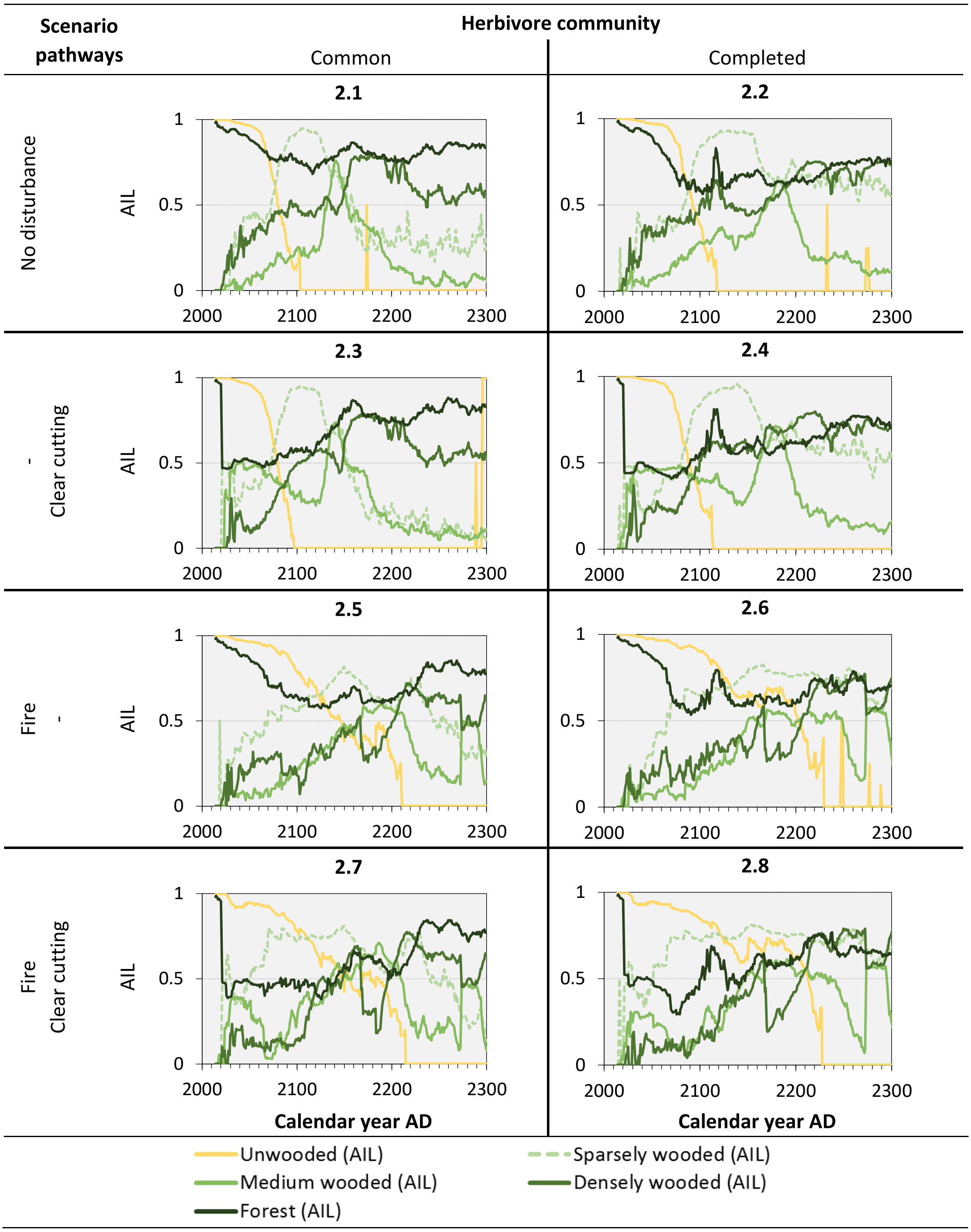



Figure 9-continued **Forest-edge scenario**

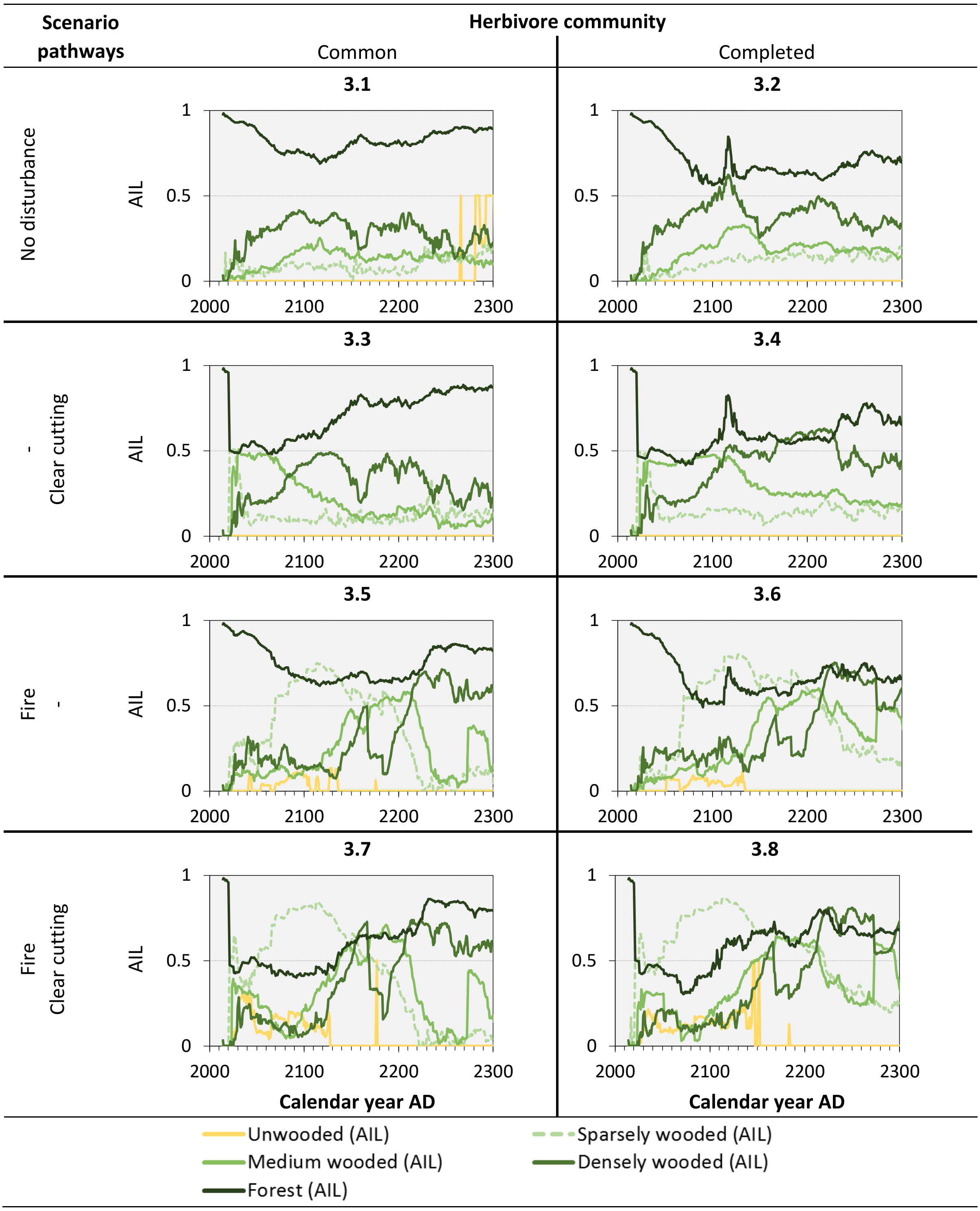



Figure 9-continued **Forest scenario**

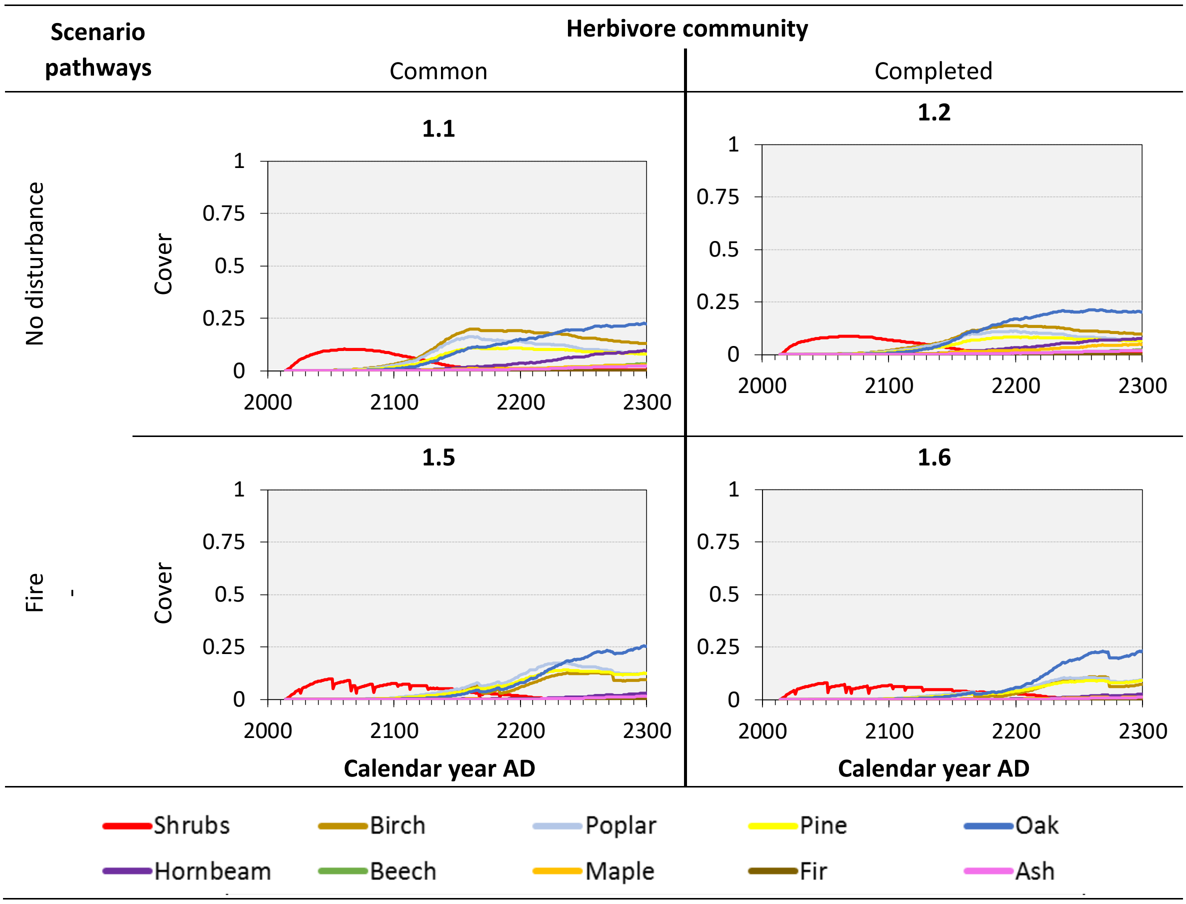



Figure 10 (including the following two pages) Trajectories of woody species cover for all scenarios, this page: **open landscape scenario**. Note that y-axis does not reach 100%, because oak and pine forests have naturally thin canopies. Woody species are beech: Buche (*Fagus sylvatica*); hornbeam: Hainbuche (*Carpinus betulus*); oak: Traubeneiche (*Quercus petraea*); pine: Waldkiefer (*Pinus sylvestris*); birch: Hängebirke (*Betula pendula*); poplar: Zitterpappel (*Populus tremula*); shrub: Heide (*Calluna vulgaris*) und Ginster (*Cytisus scoparius*). In this figure, the **open landscape** scenario pathways are shown.

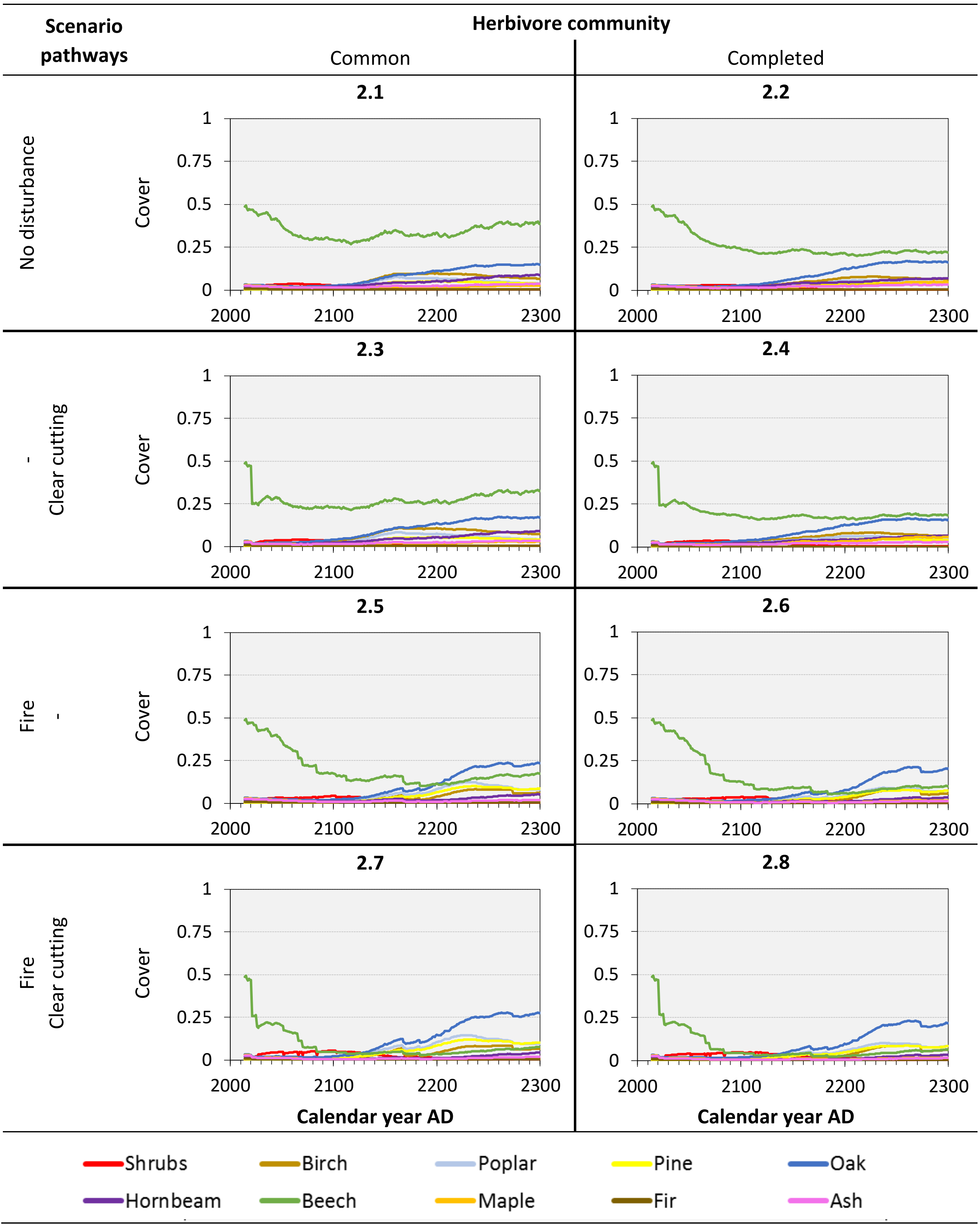



Figure 10-continued **Forest edge scenario**

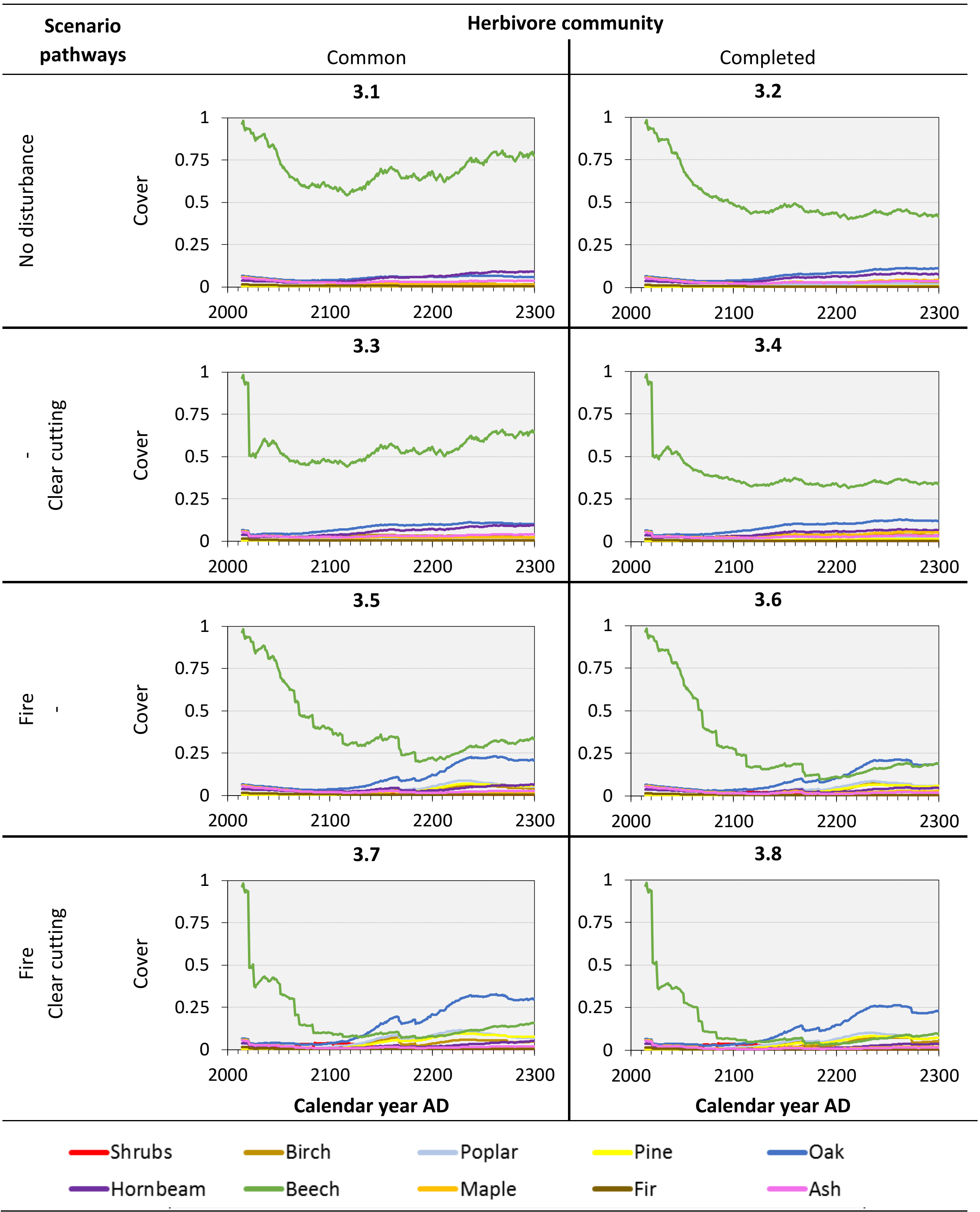



Figure 10-continued **Forest scenario**

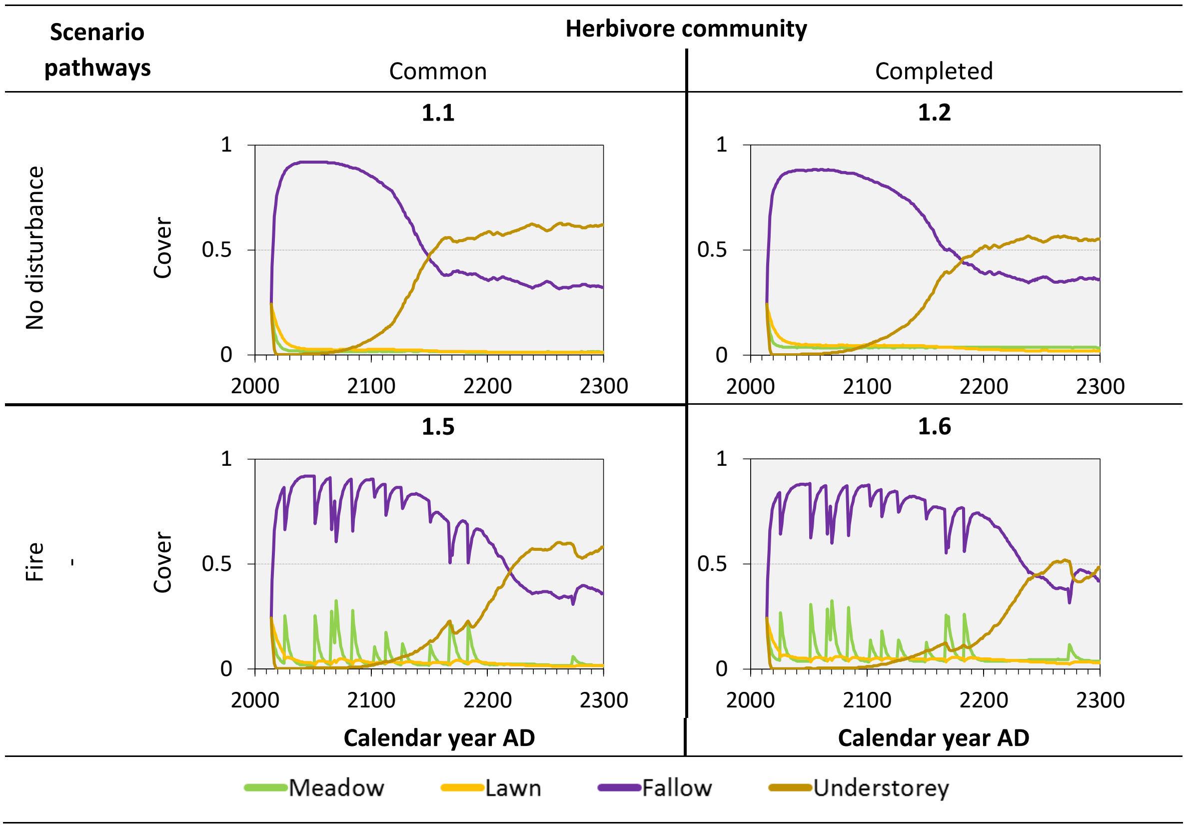



Figure 11 (including the following two pages) Trajectories of the cover of vegetation types in herb layer for all scenarios. For the definition of herb layer vegetation types refer to Table 3. In this figure, the **open landscape** scenario pathways are shown.

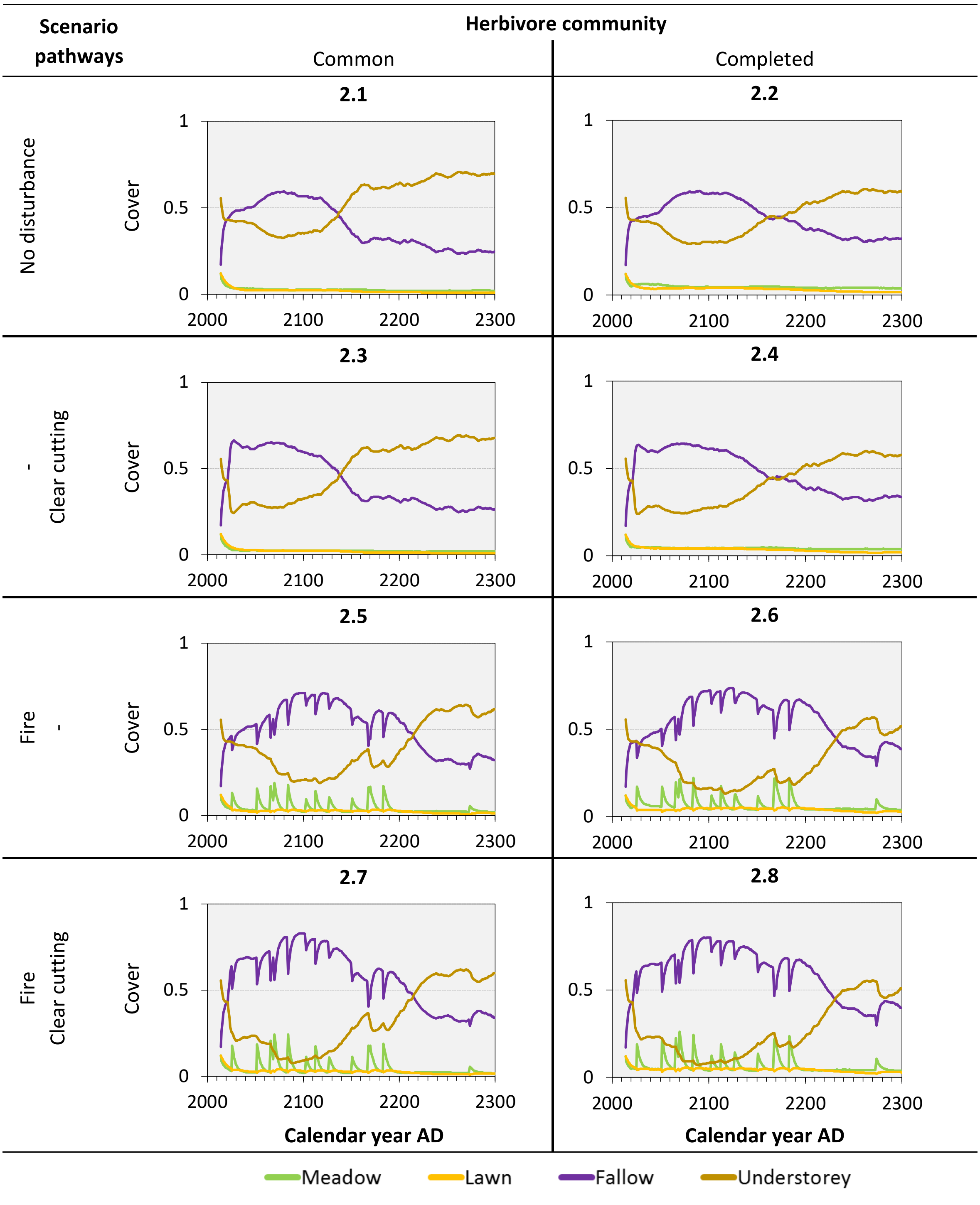



Figure 11-continued **Forest edge scenario**

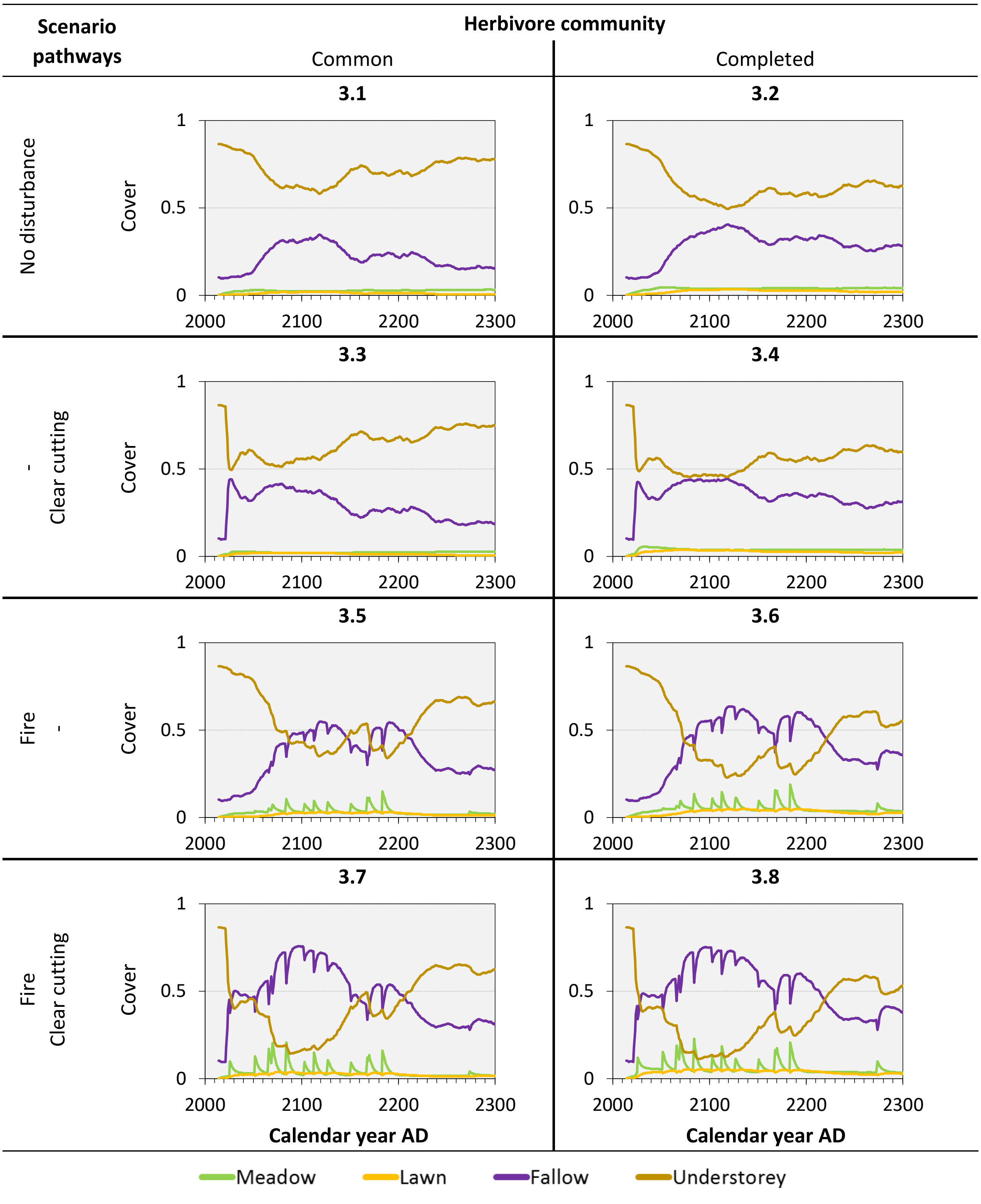



Figure 11-continued **Forest scenario**

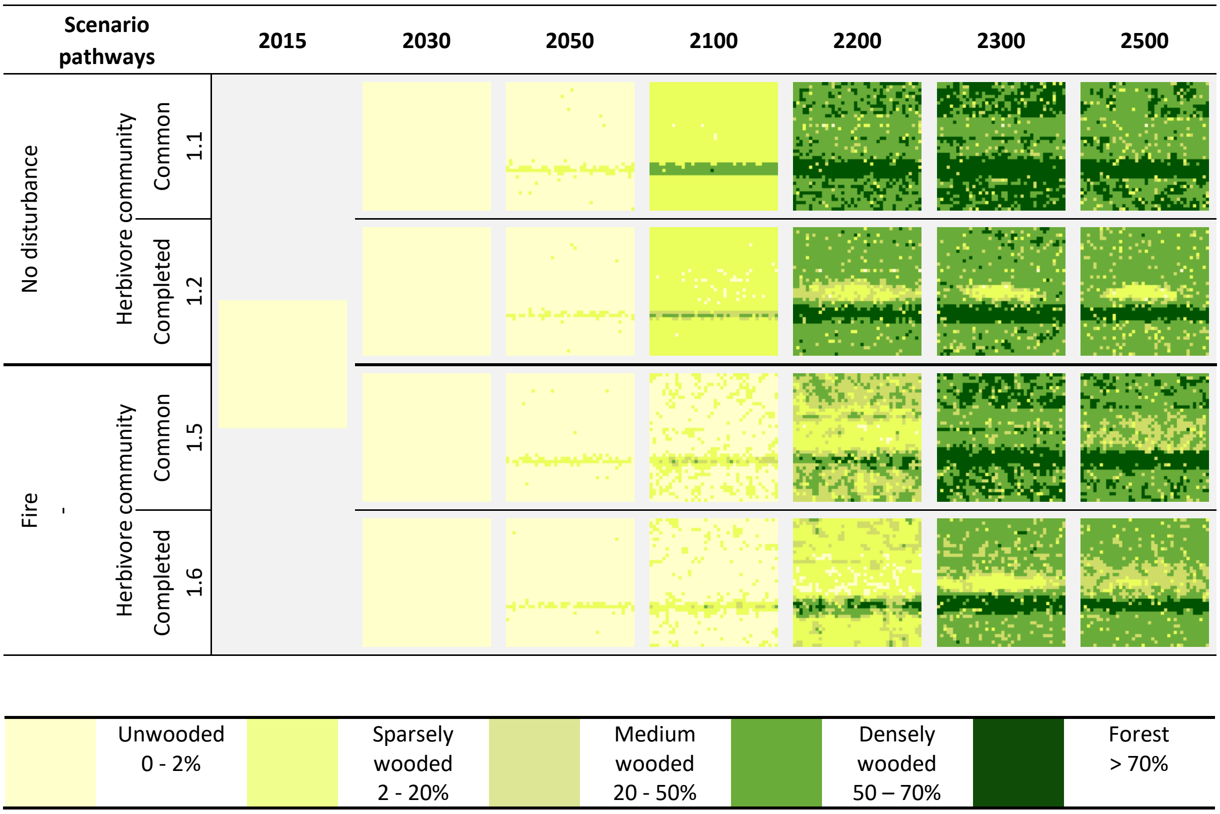



Figure 12 (including the following two pages) Landscape-structural change in terms of the spatial distribution of habitat types (refer to Table 2) during scenario simulations. The maps show the initial states (1990 AD), short- and medium-term developments (2030 and 2050 AD), the development until the end of the climate change scenario and for approximately one tree generation (2100 AD) and long-term projections under end-of-2100-climatic conditions that aim to pinpoint successional trends (2200, 2300 and 2500 AD). In this figure, the **open landscape** scenario pathways are shown.

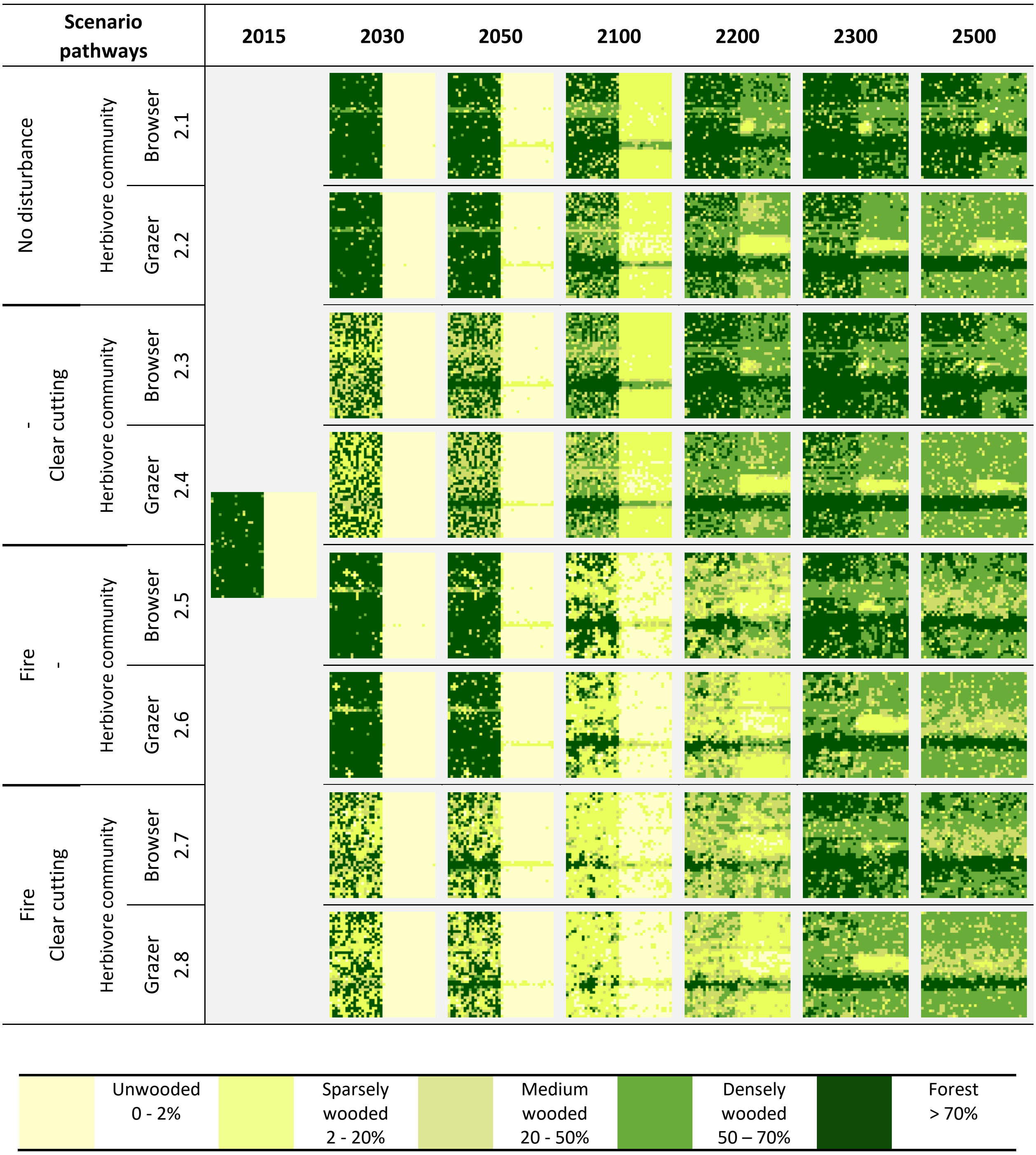



Figure 12-continued **Forest edge scenario**

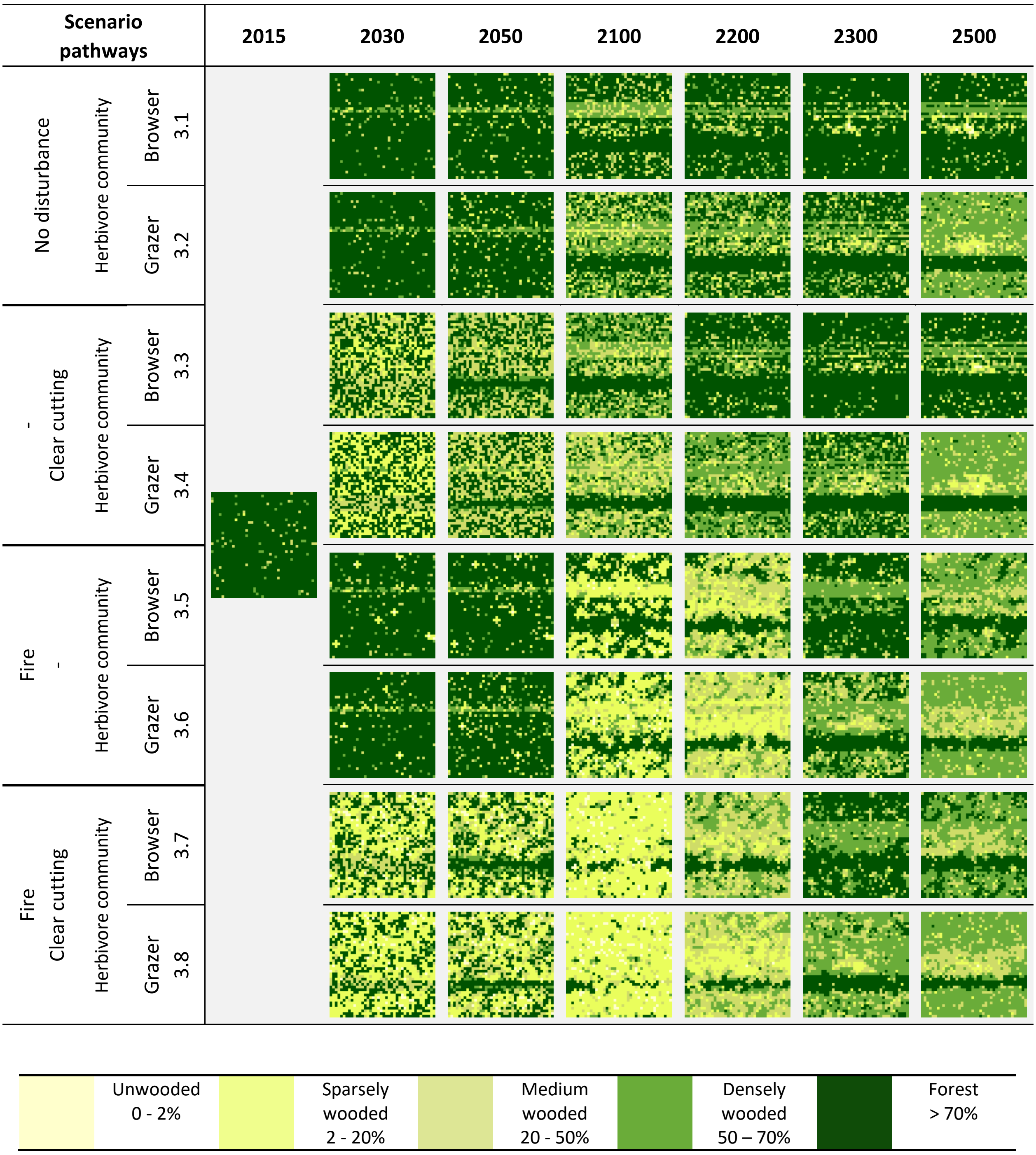



Figure 12-continued **Forest scenario**

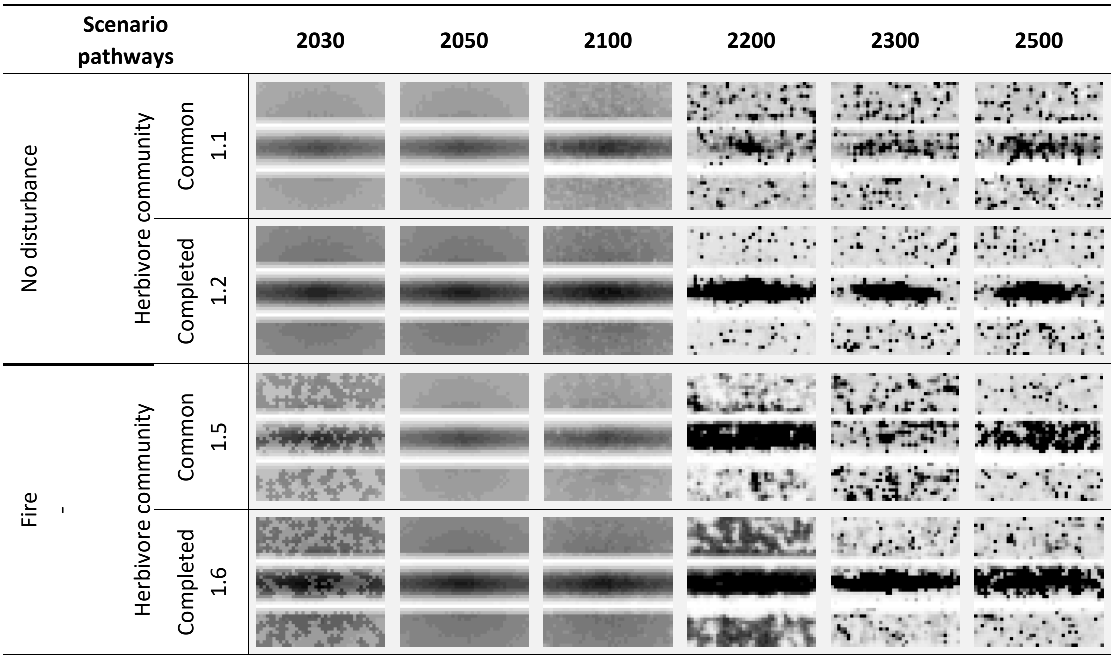



Figure 13 (including the following two pages) Dynamics of grazing patterns in the scenario simulations with herbivores. We show solely grazing and skip Browser, because open landscape habitats depend on grazing rather than Browser. In this figure, the **open landscape** scenario pathways are shown.

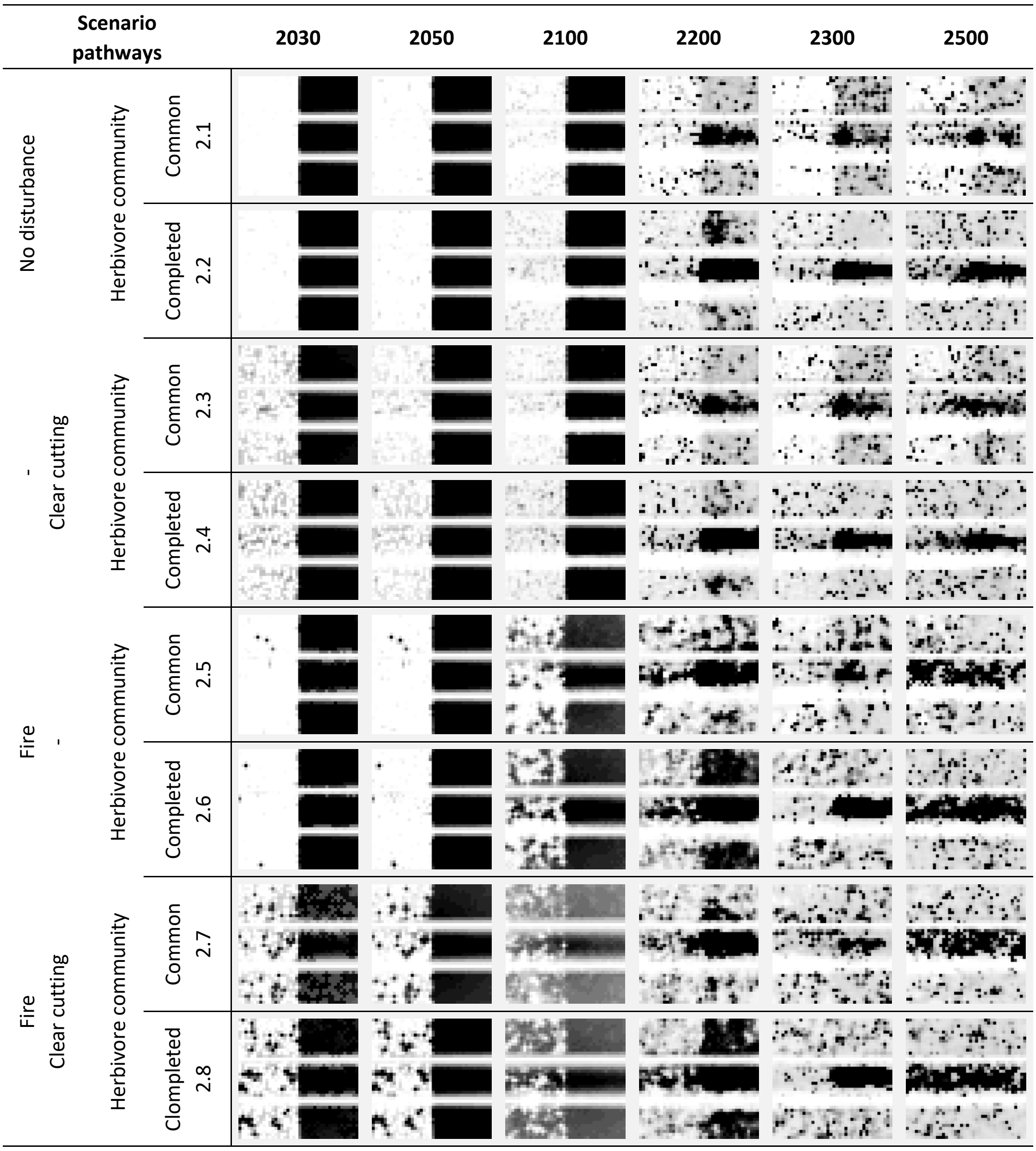



Figure 13-continued **Forest edge scenario**

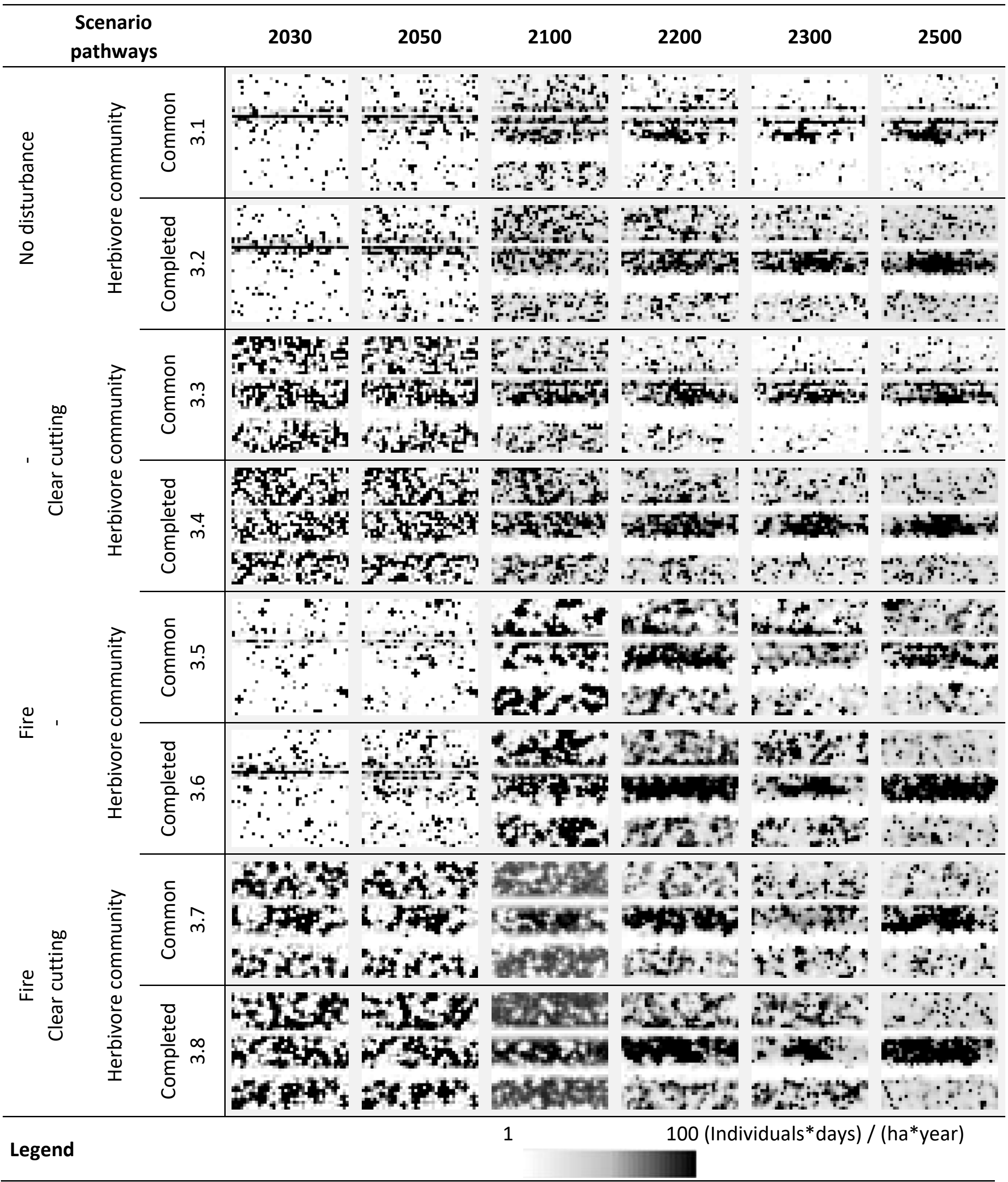



Figure 13-continued **Forest scenario**

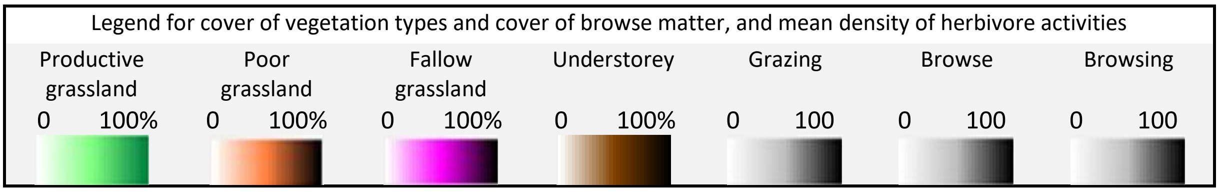
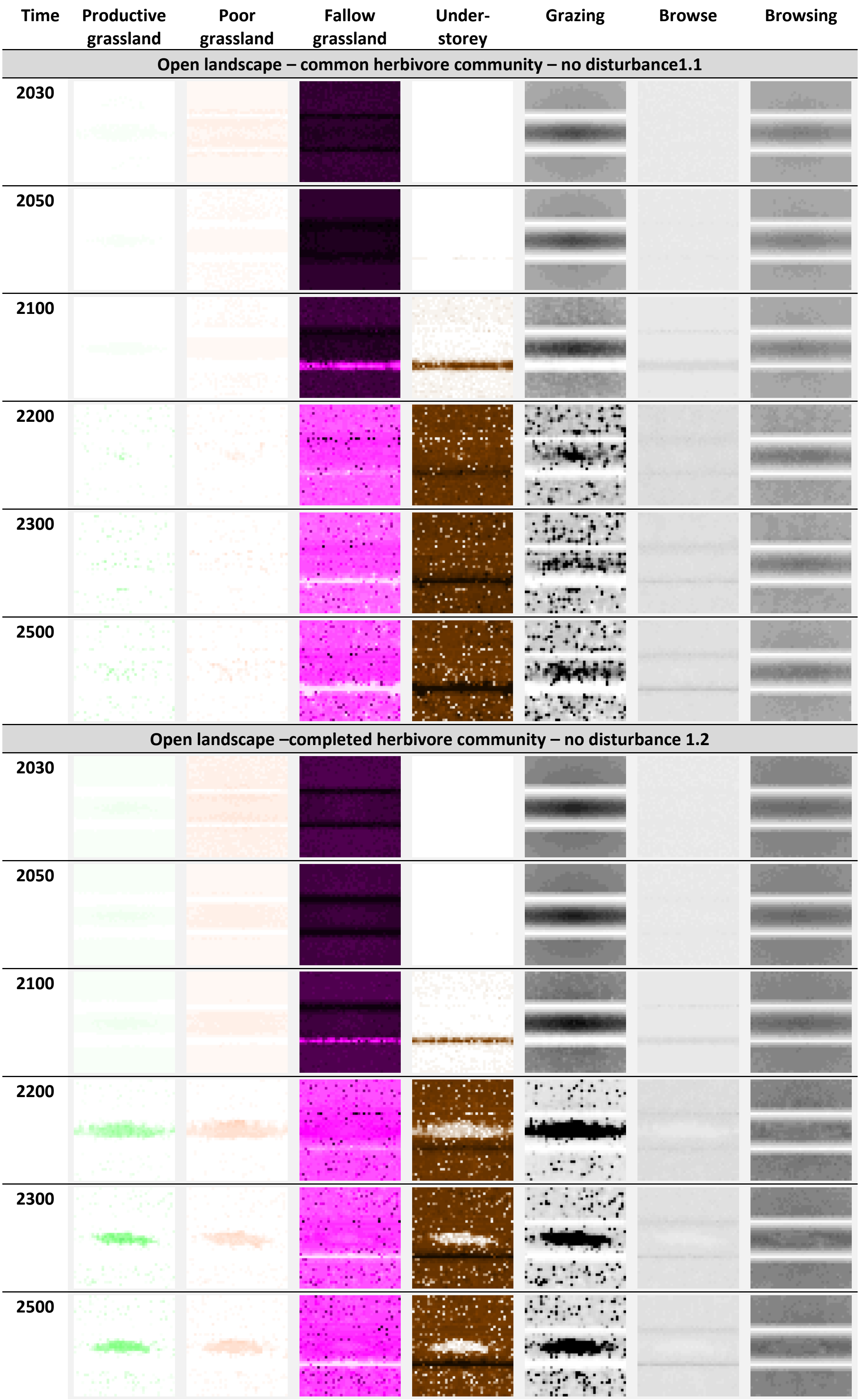



Figure 14 The following five pages show the phytodiversity of the herb layer (in terms of cover of vegetation types), the cover of browse and corresponding habitat use of herbivores for grazing and Browser in all herbivore scenarios including fire and clear cutting. The legend is shown above. Herb layer vegetation (“productive grassland”, poor grassland”, “fallow grassland” and “understorey”) determines the amount and quality of herbaceous forage and thereby herbivores’ habitat use for grazing (darker grey tones indicate more Individuals * days per hectare in a grid cell). The amount and quality of woody browse was derived from tree sapling and shrub cover and determines herbivores’ habitat use for Browser (darker grey tones indicate more Individuals * days per hectare in a grid cell).


Time
Productive grassland
Poor grassland
Fallow grassland
Under-storey
Grazing
Browse
Browsing
Open landscape – common herbivore community – no disturbance1.1
2030
2050
2100
2200
2300
2500
Open landscape –completed herbivore community – no disturbance 1.2
2030
2050
2100
2200
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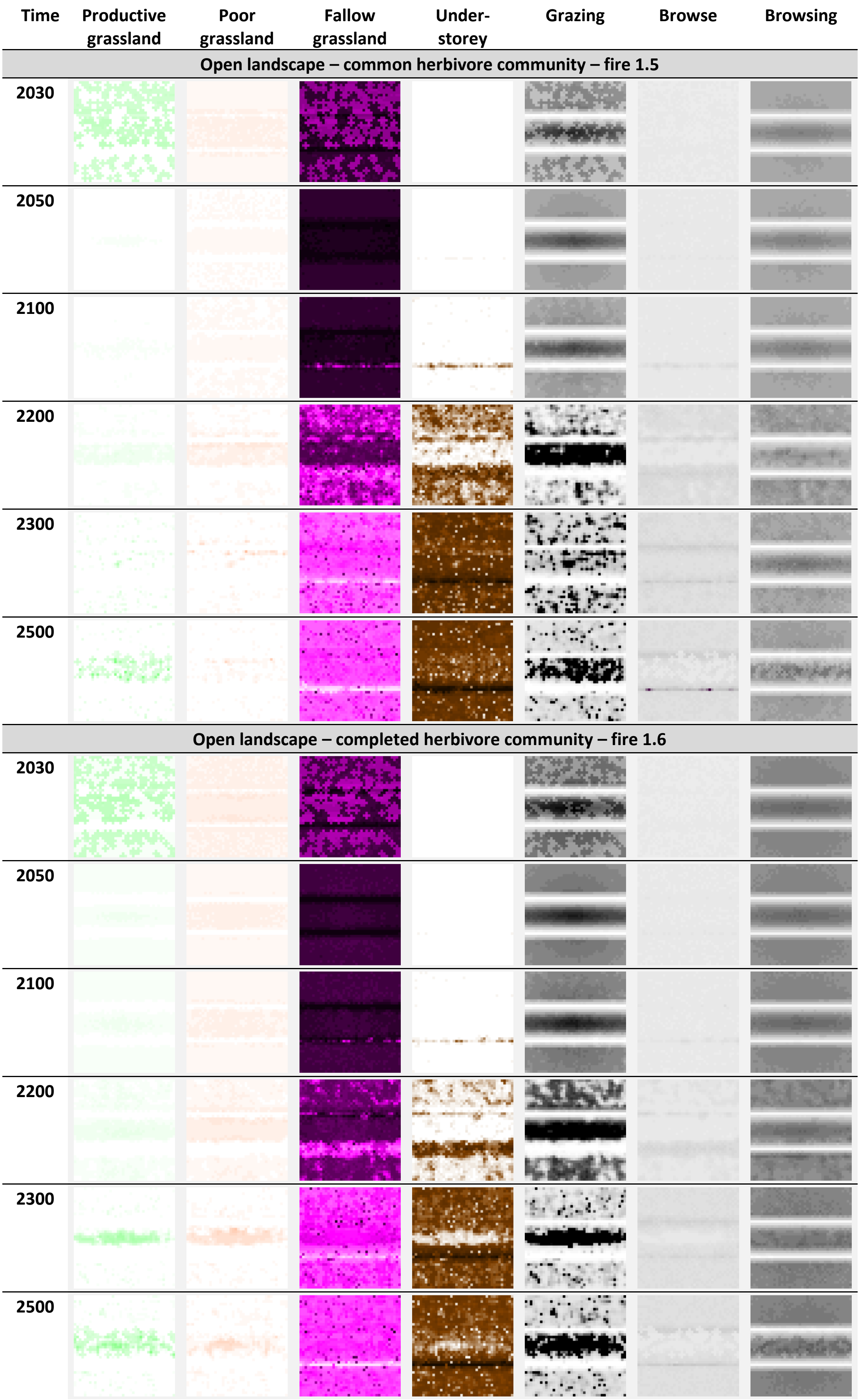
Time
Productive grassland
Poor grassland
Fallow grassland
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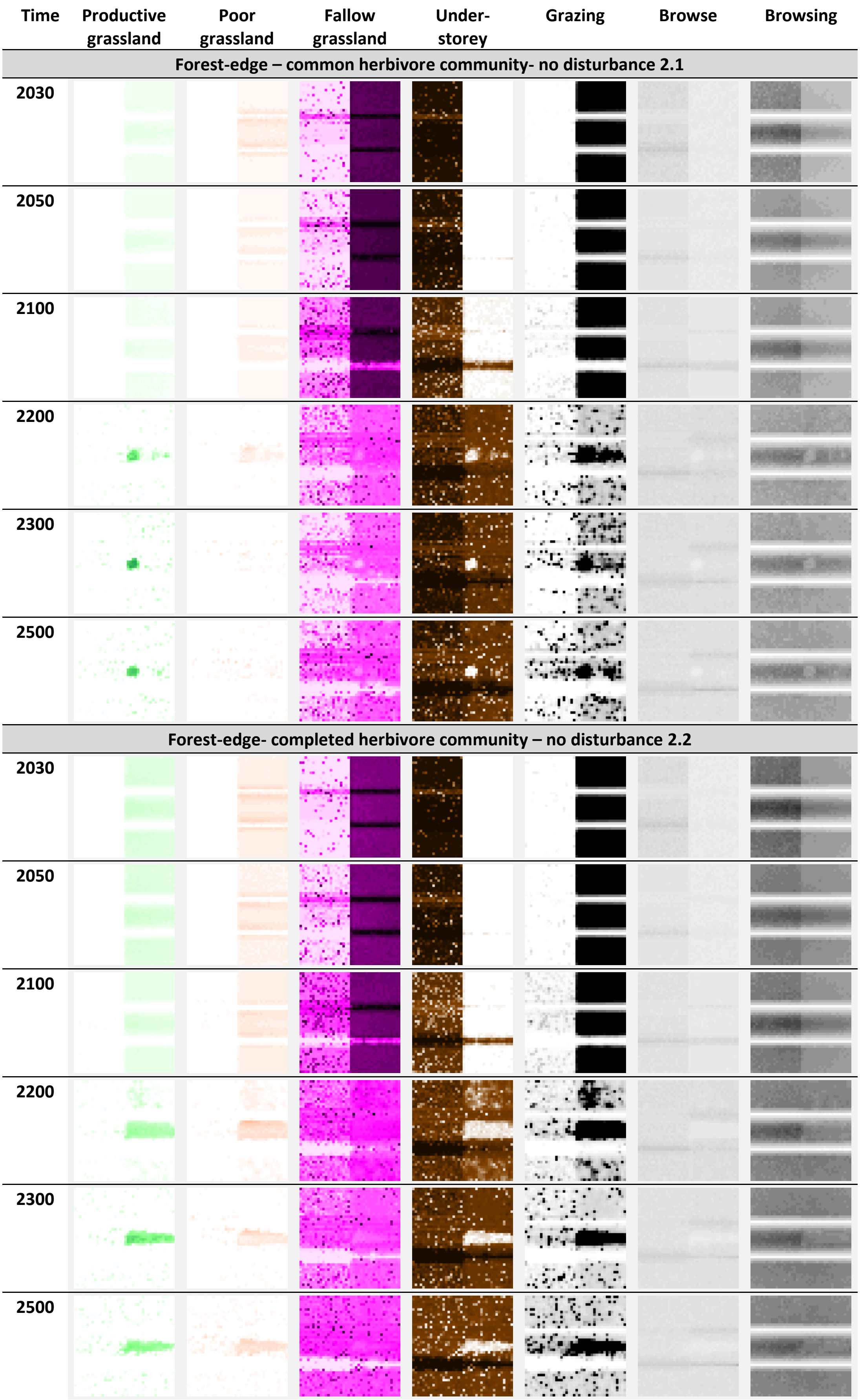
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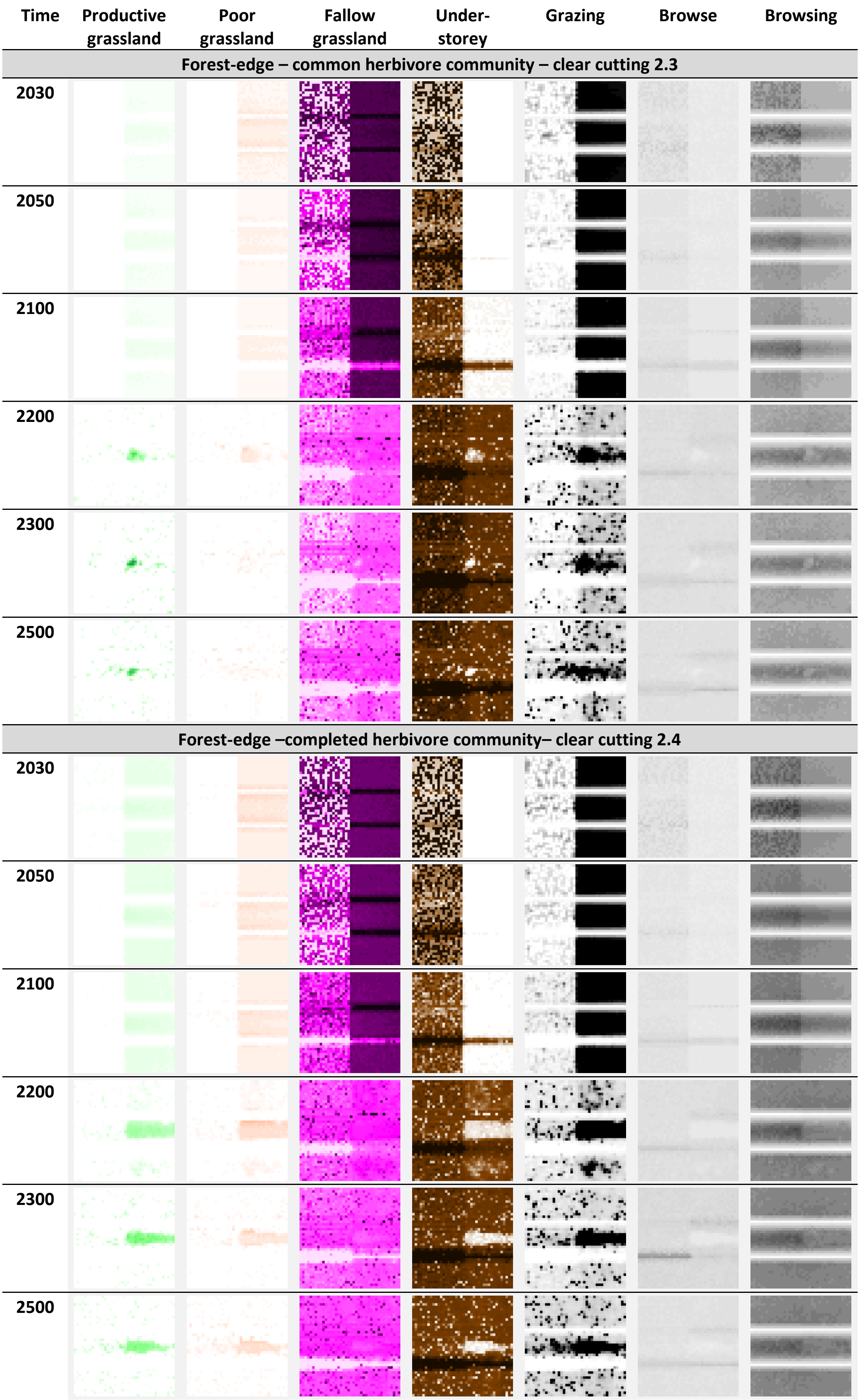
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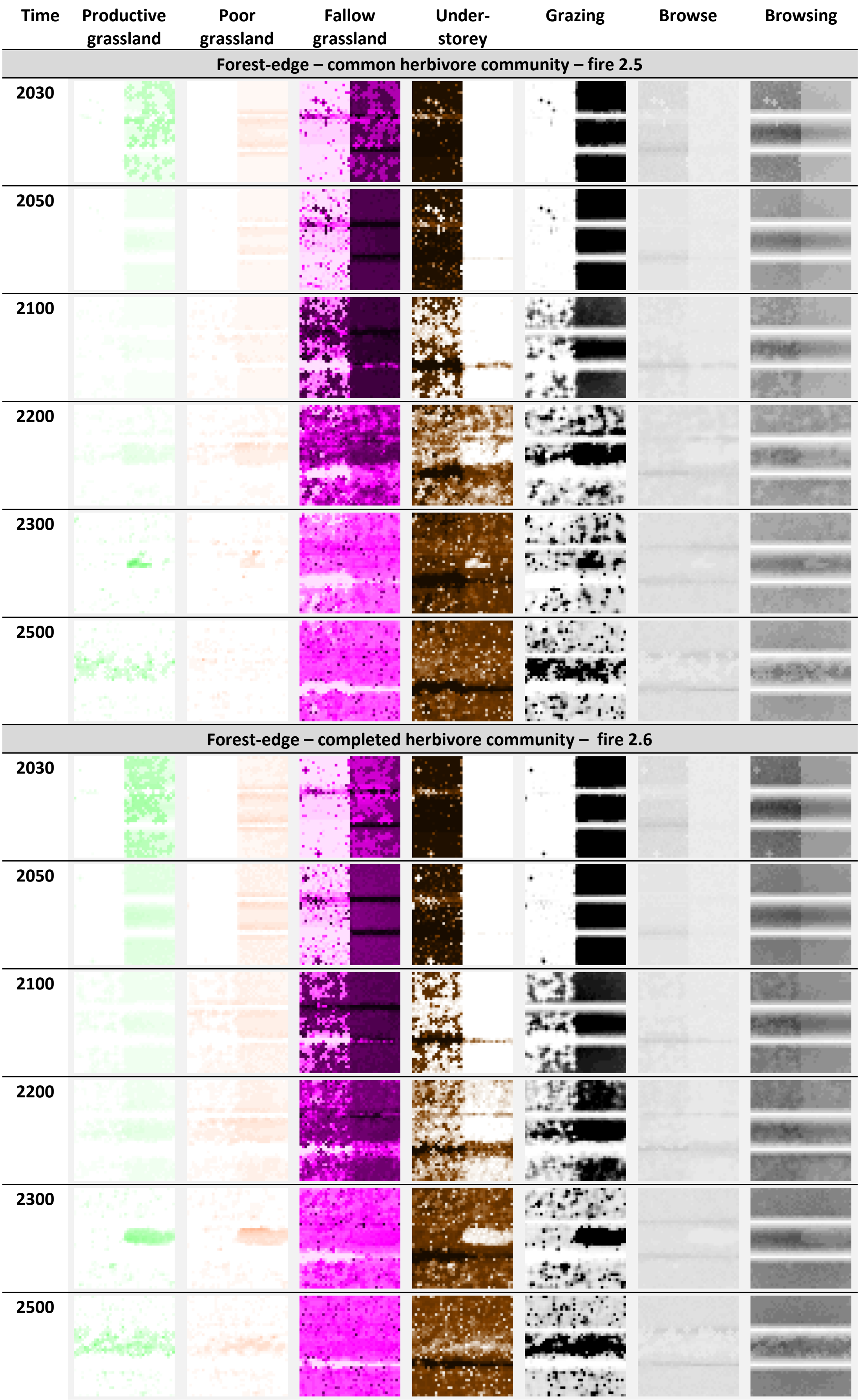
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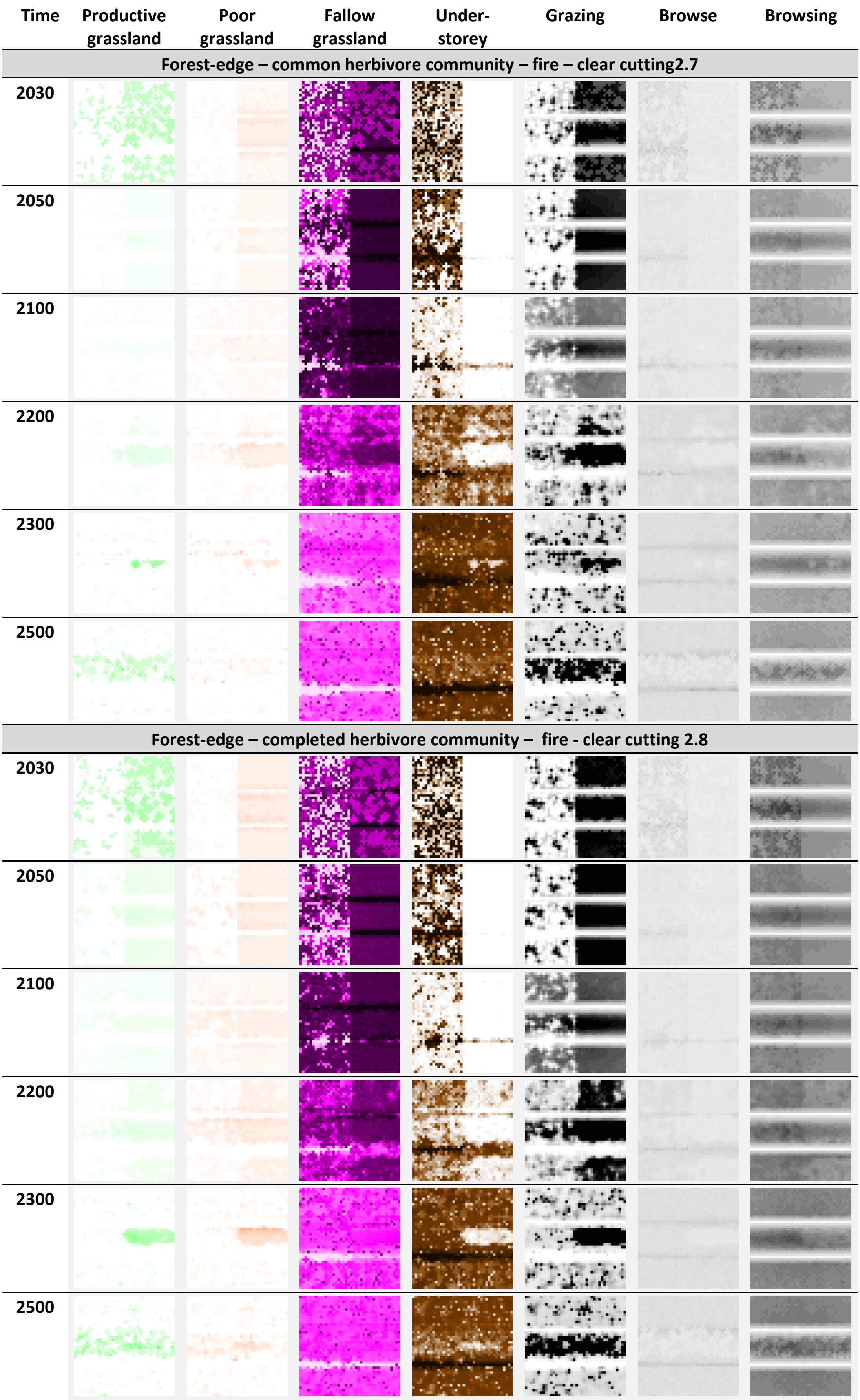

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Forest-edge – completed herbivore community – fire - clear cutting 2.8
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| Time | Productive grassland | Poor grassland | Fallow grassland | Under-storey | Grazing | Browse | Browsing |
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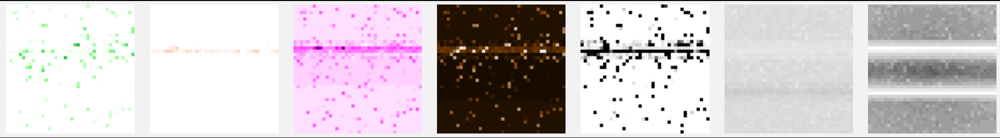
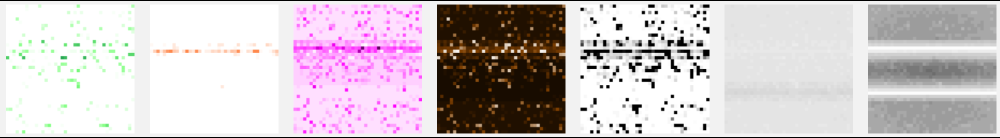
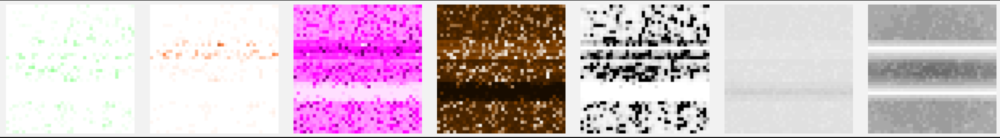
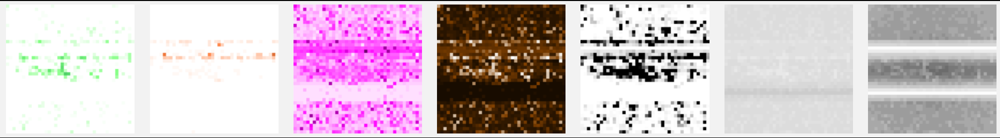
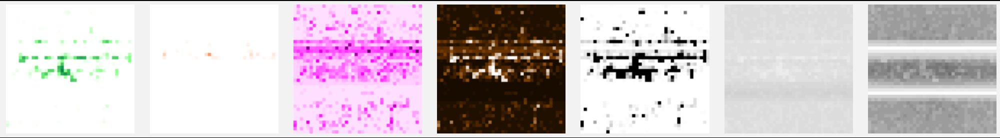
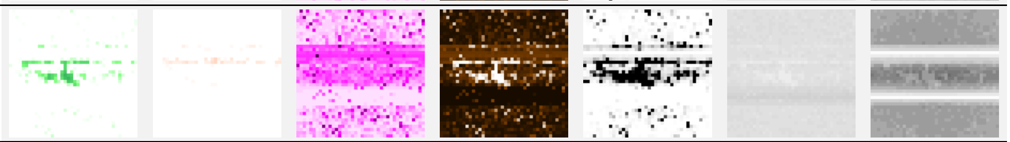
| **2030** |  | | | | | | |
| **2050** |  | | | | | | |
| **2100** |  | | | | | | |
| **2200** |  | | | | | | |
| **2300** |  | | | | | | |
| **2500** |  | | | | | | |
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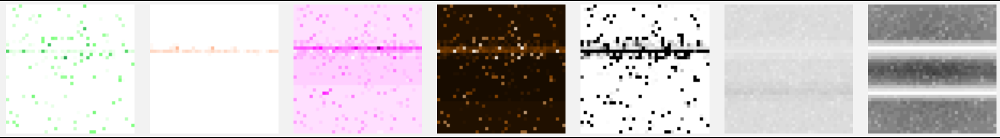
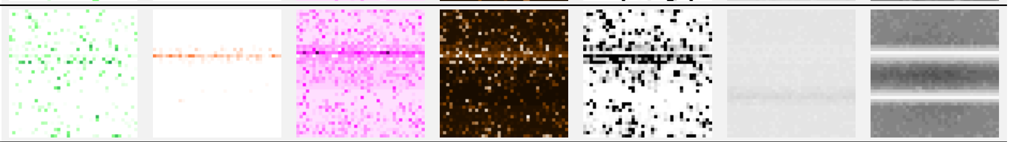
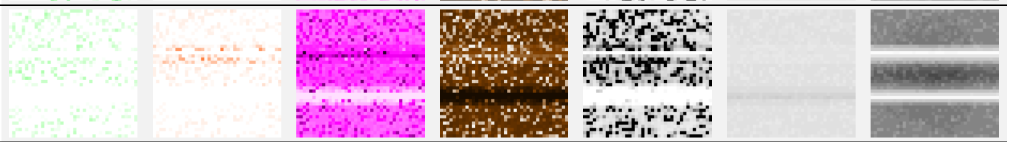
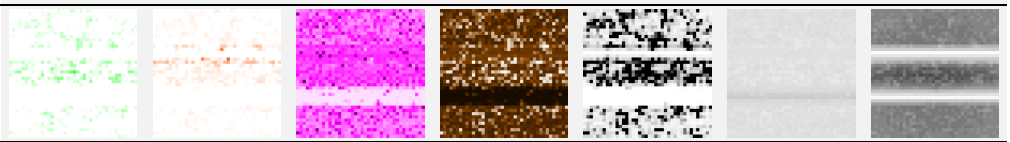
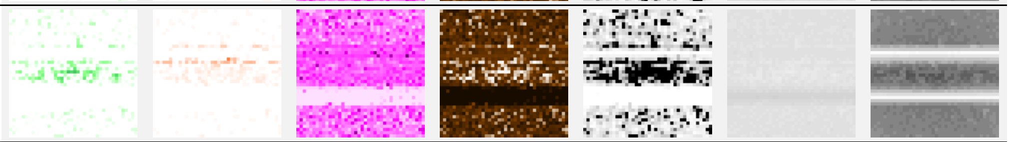
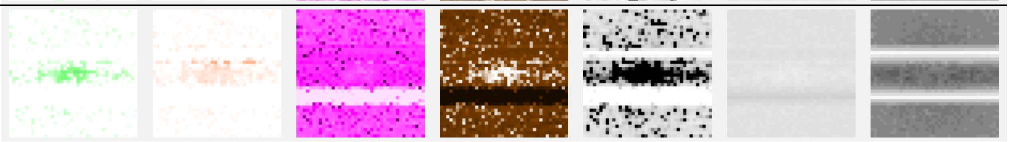
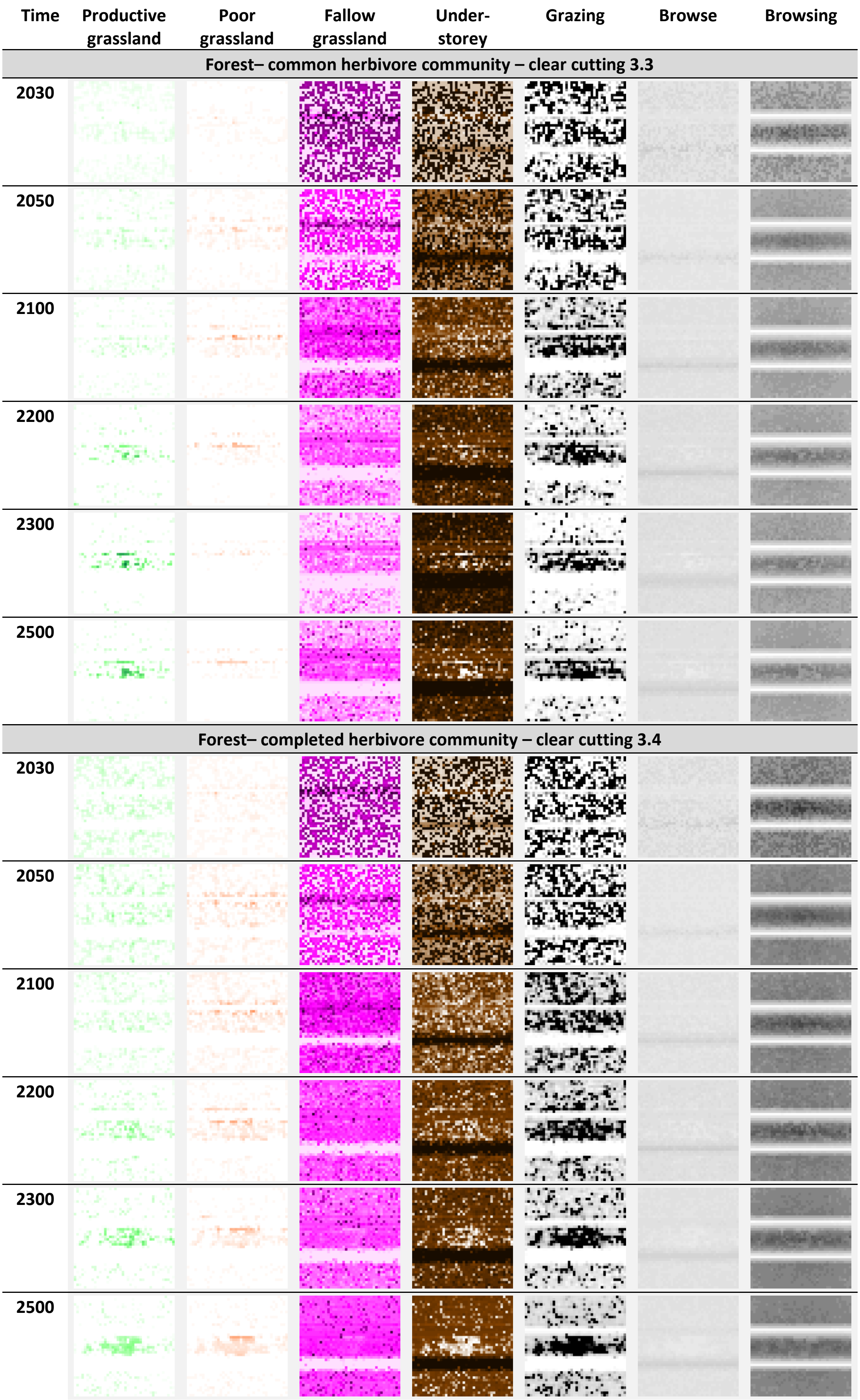
| **2030** |  | | | | | | |
| **2050** |  | | | | | | |
| **2100** |  | | | | | | |
| **2200** |  | | | | | | |
| **2300** |  | | | | | | |
| **2500** |  | | | | | | |



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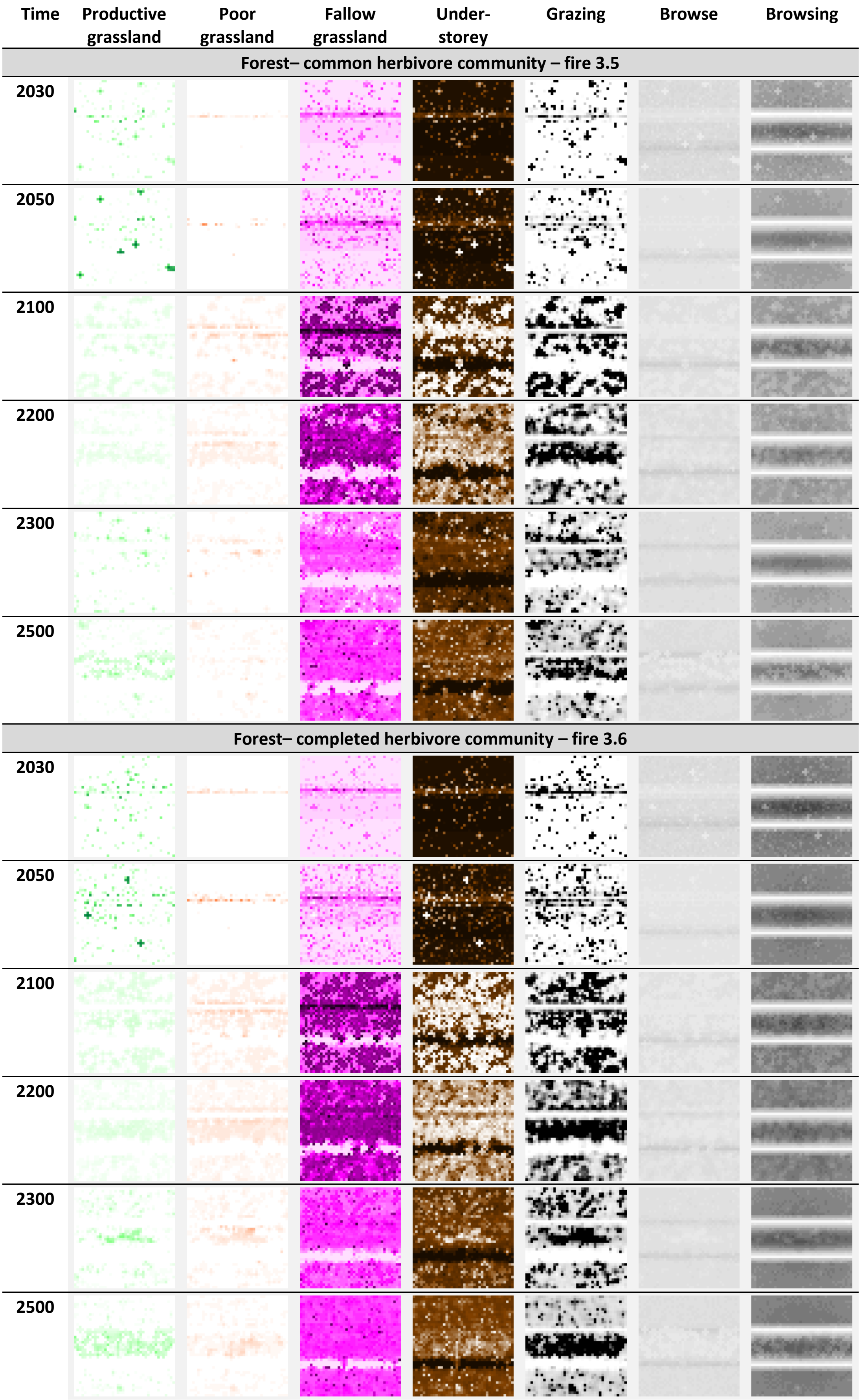
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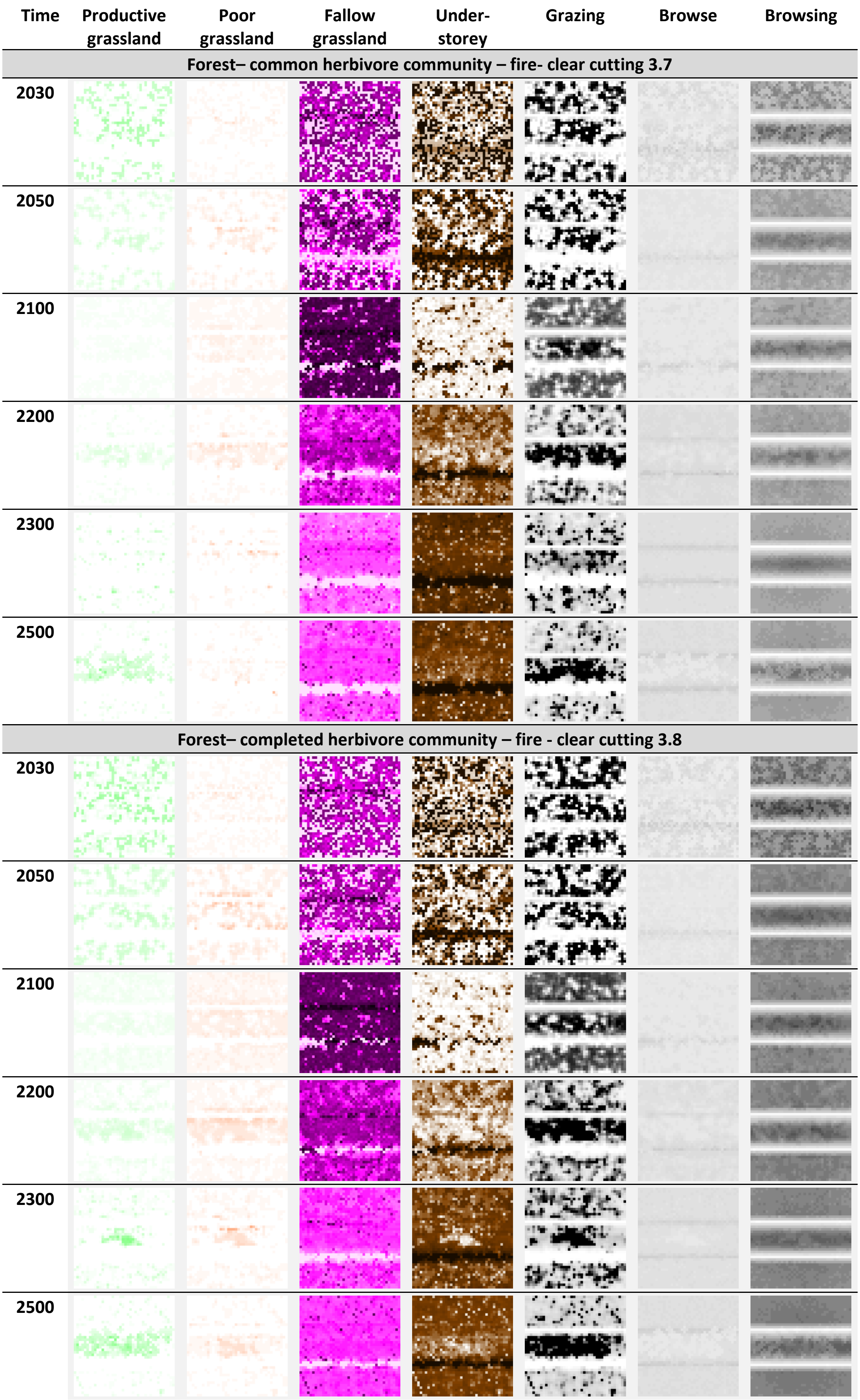
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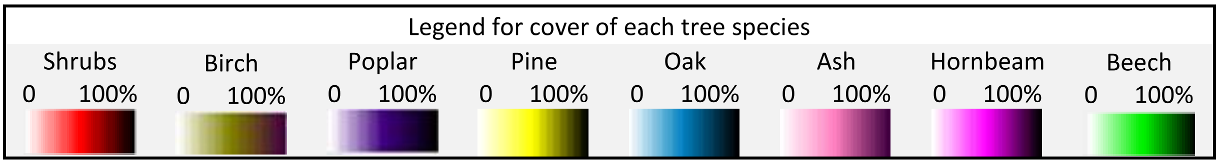
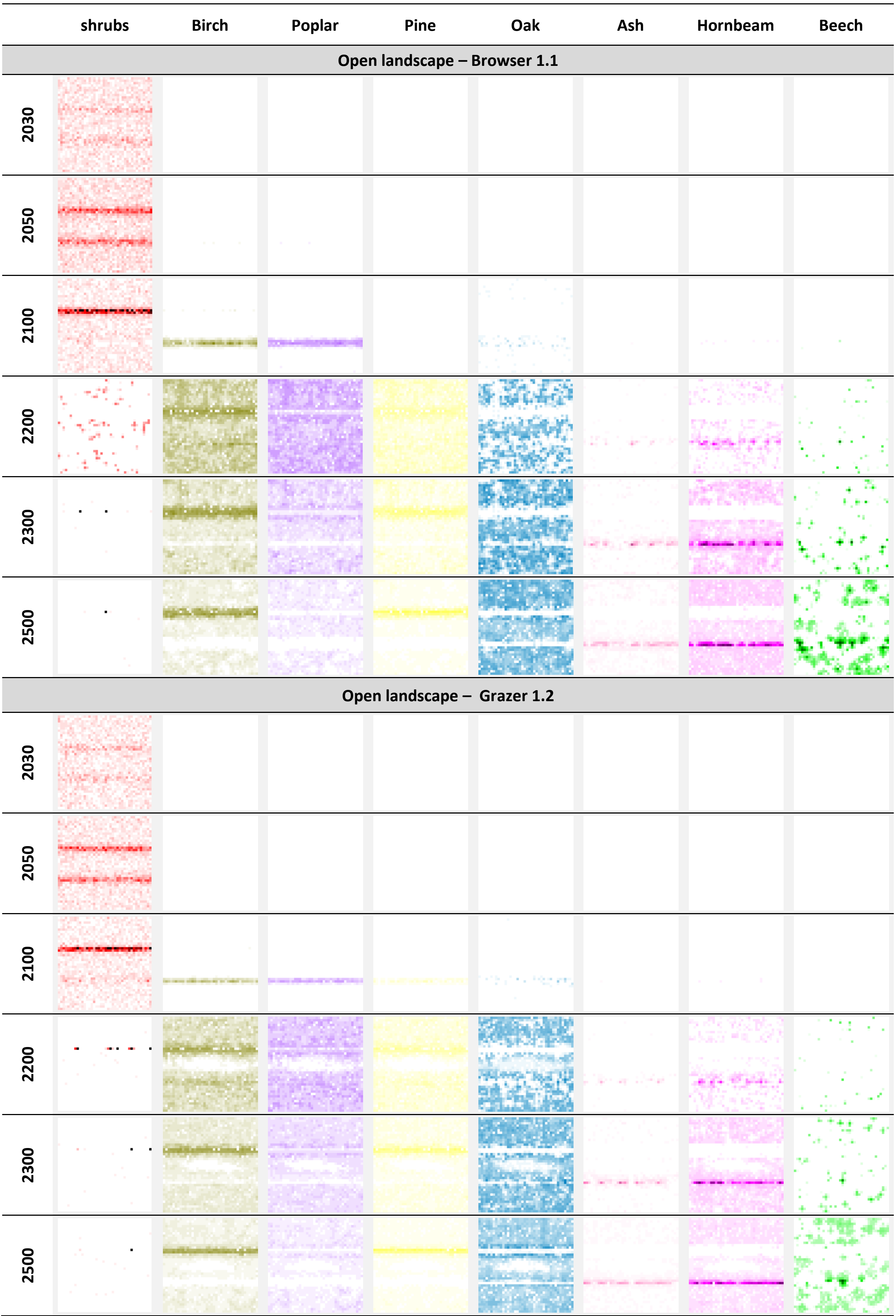
Figure 15 The following ten pages show the tree species distribution and change for all scenarios. The legend is shown below. Upper half of the page: absence of herbivores. Lower part of the page: with herbivores.

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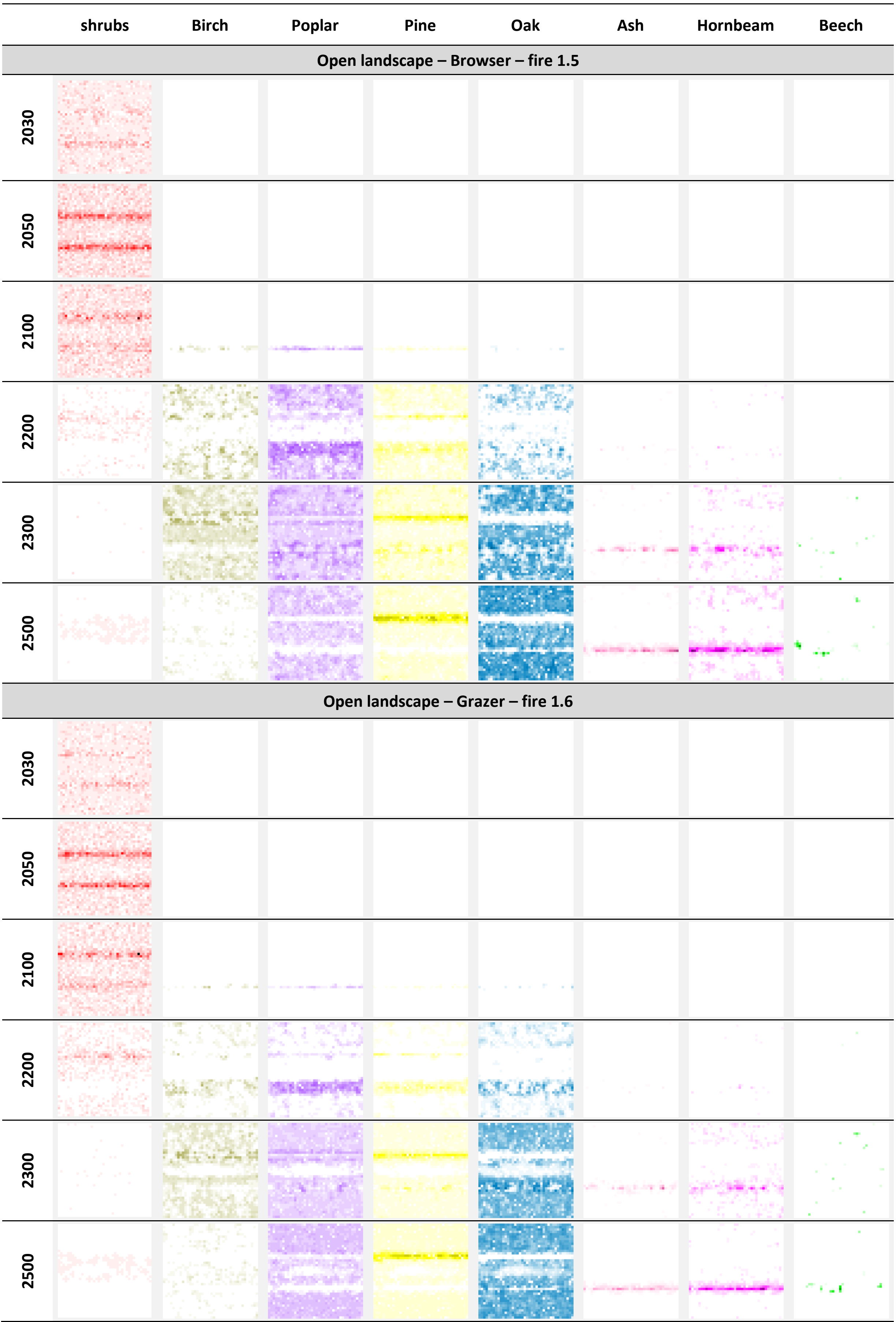
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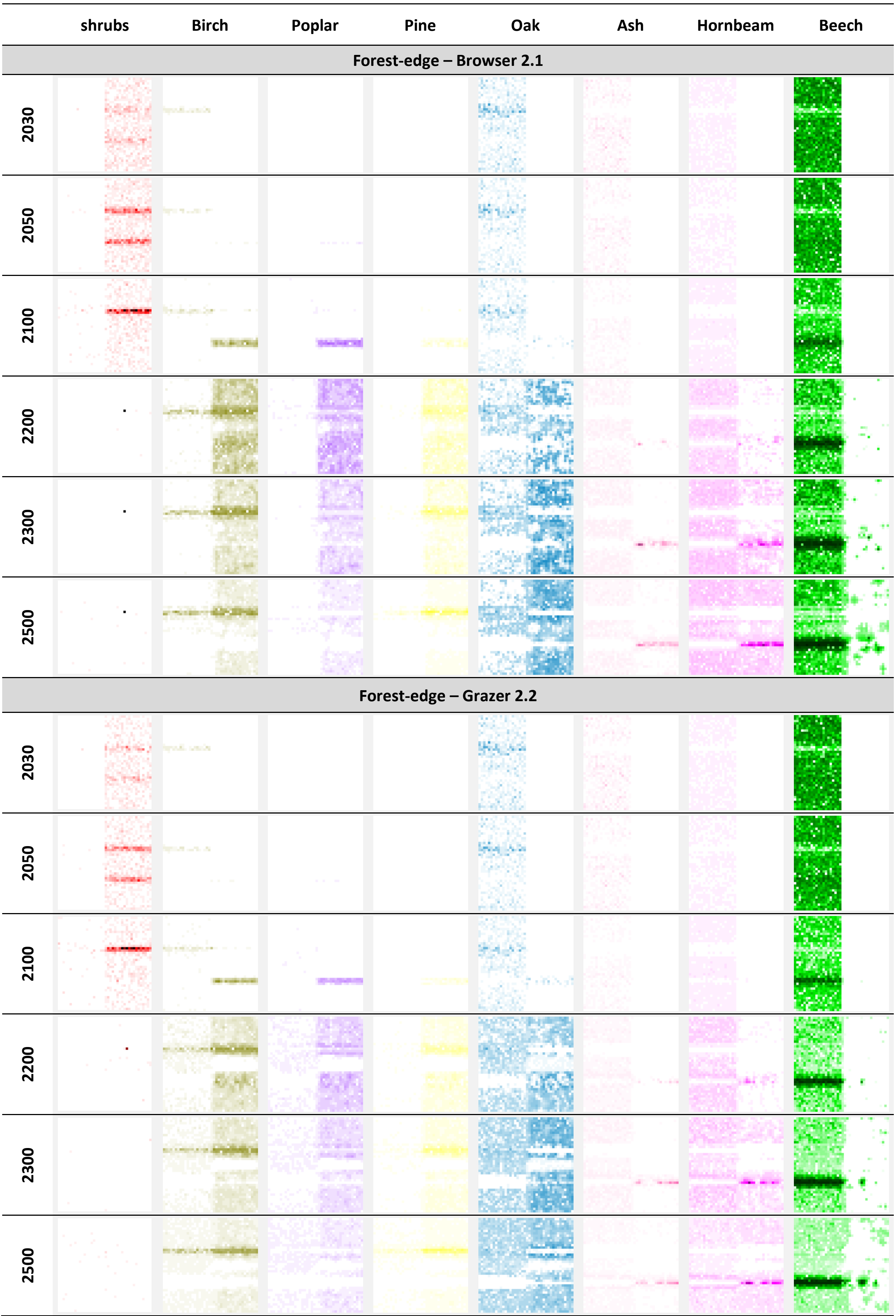
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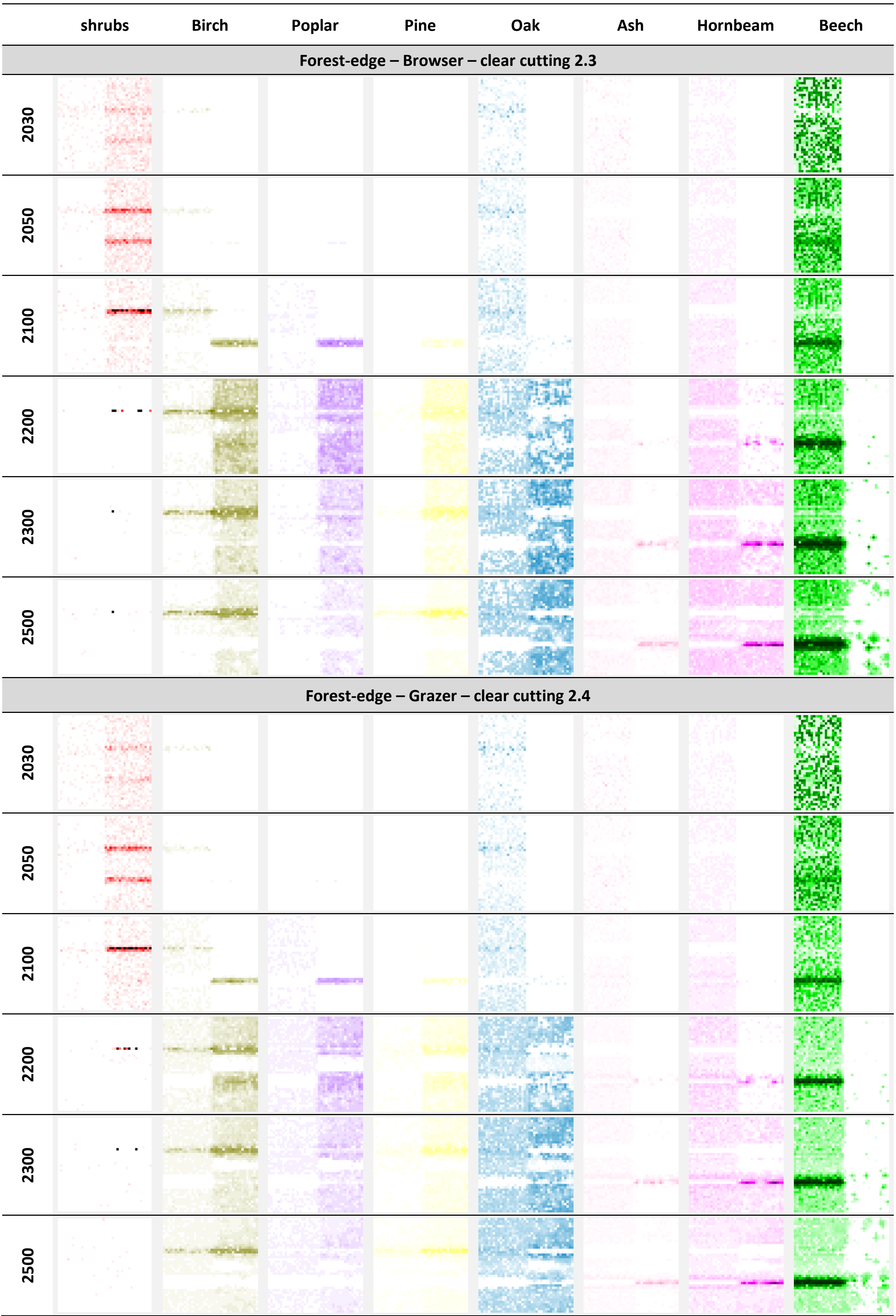
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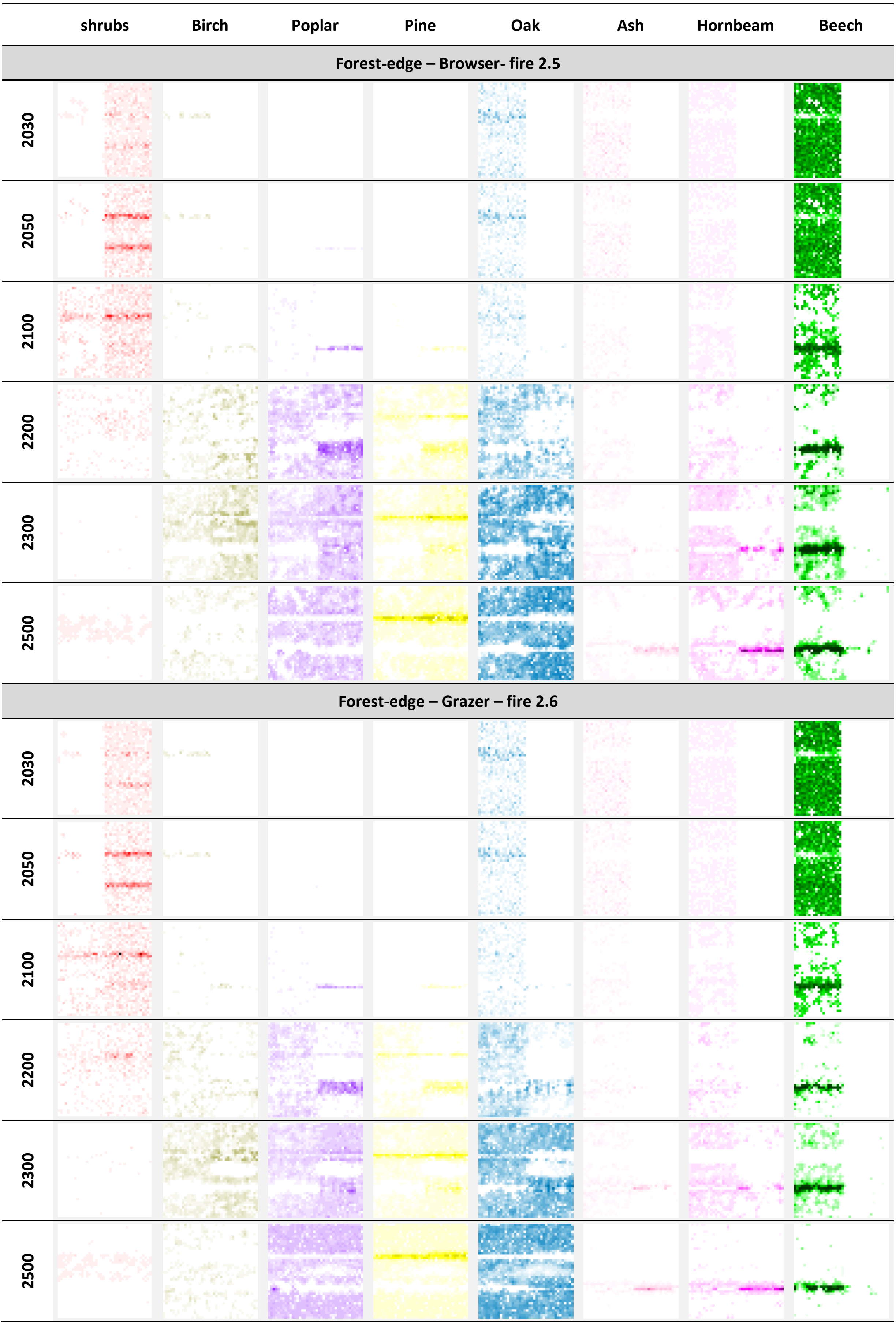

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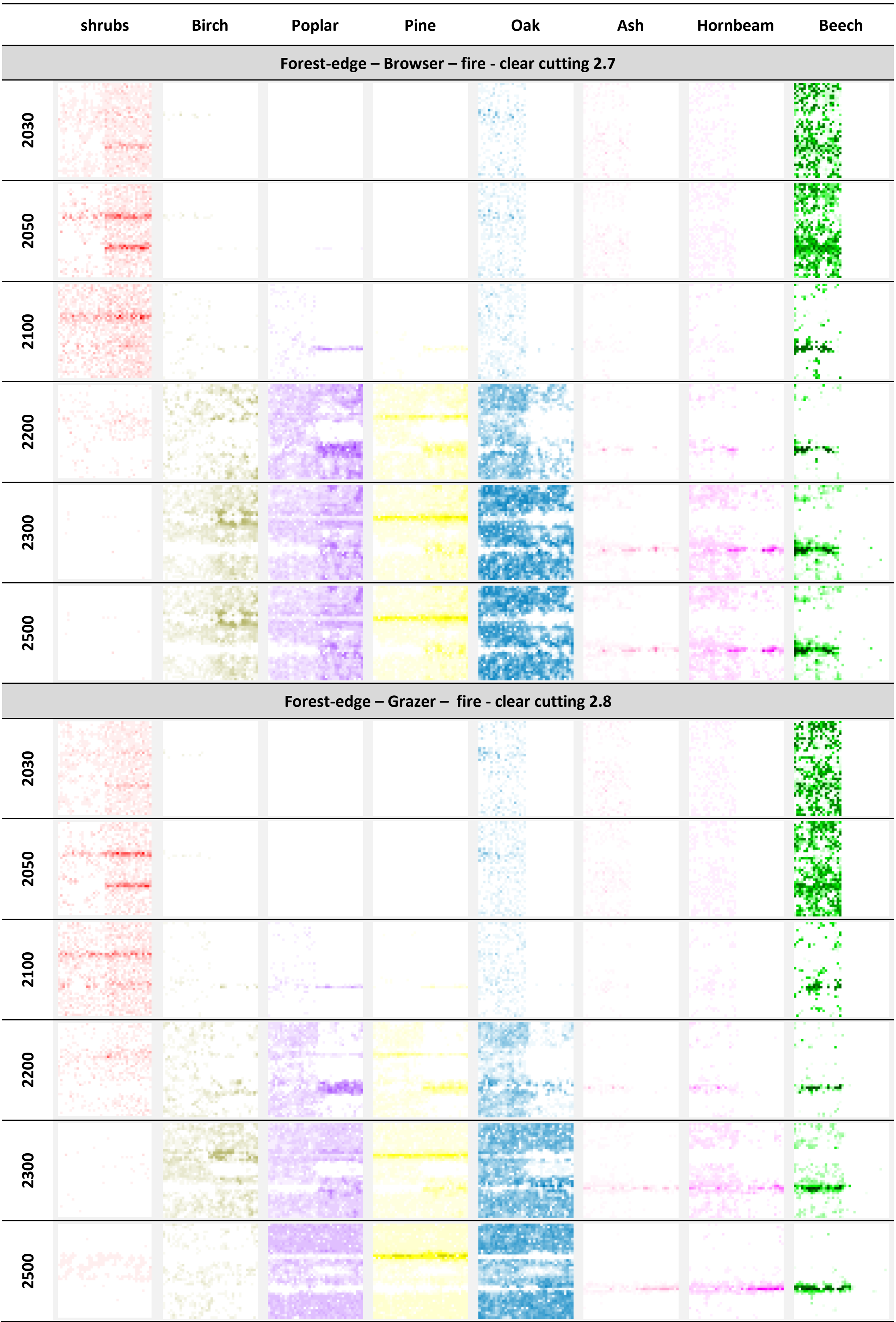
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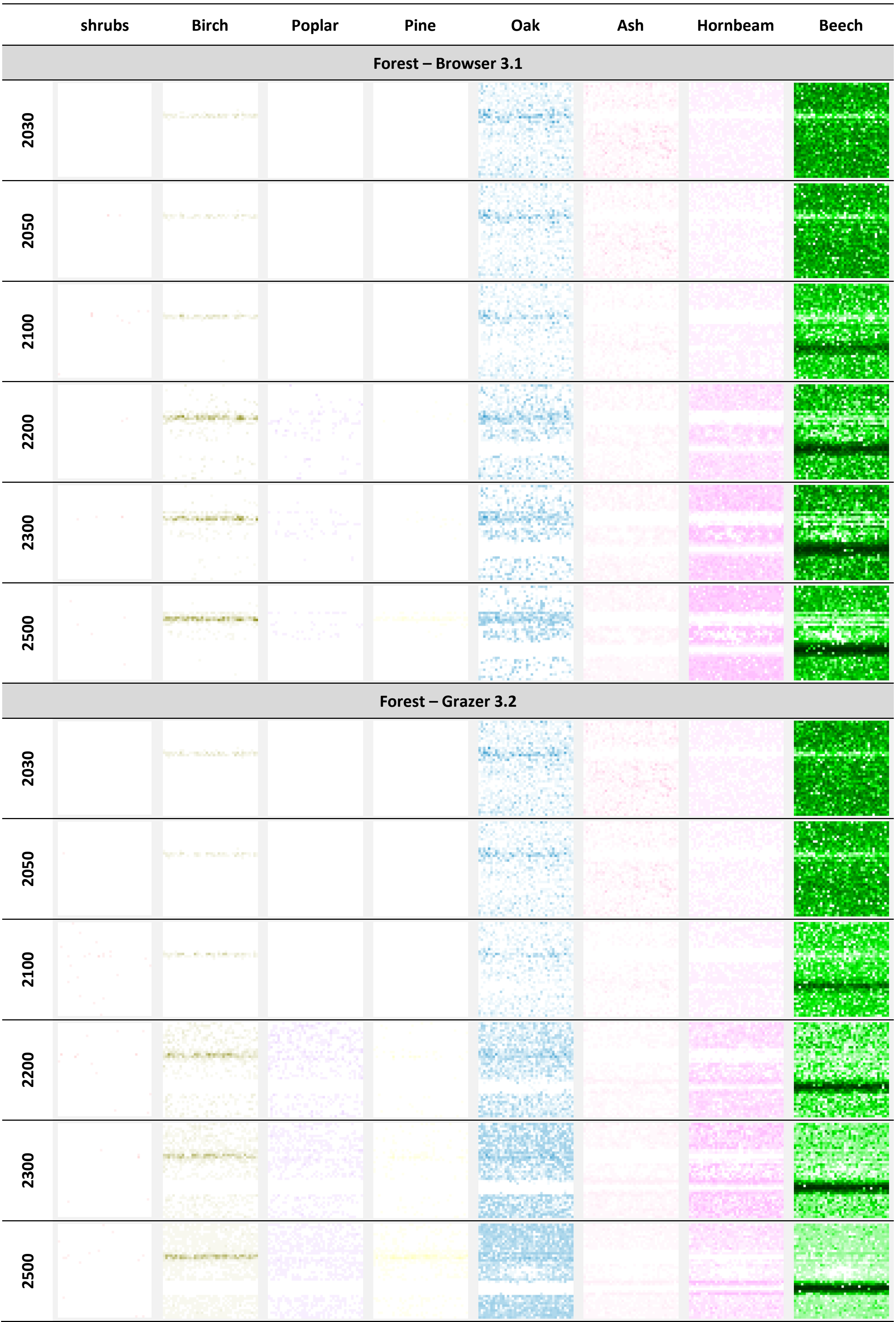

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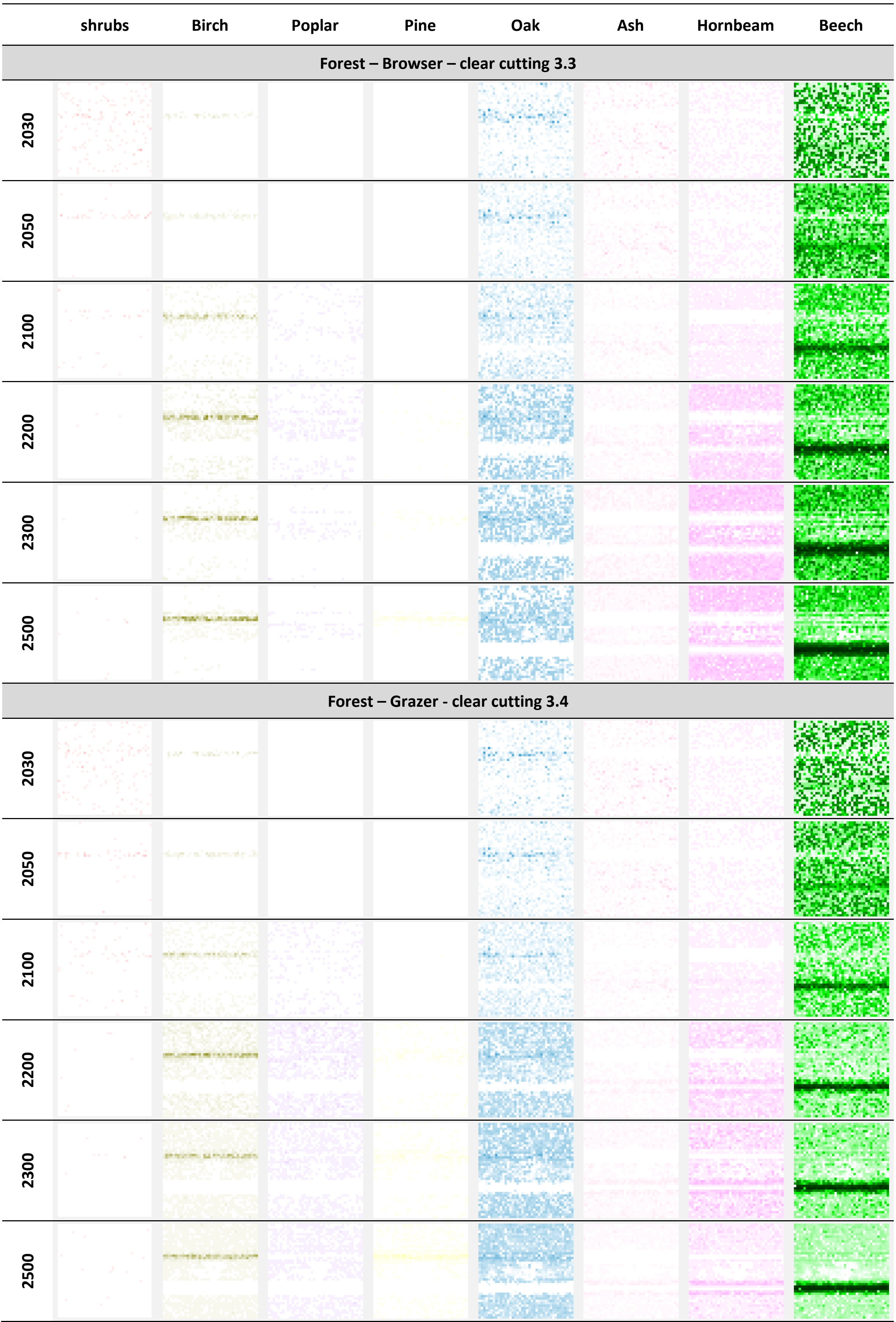
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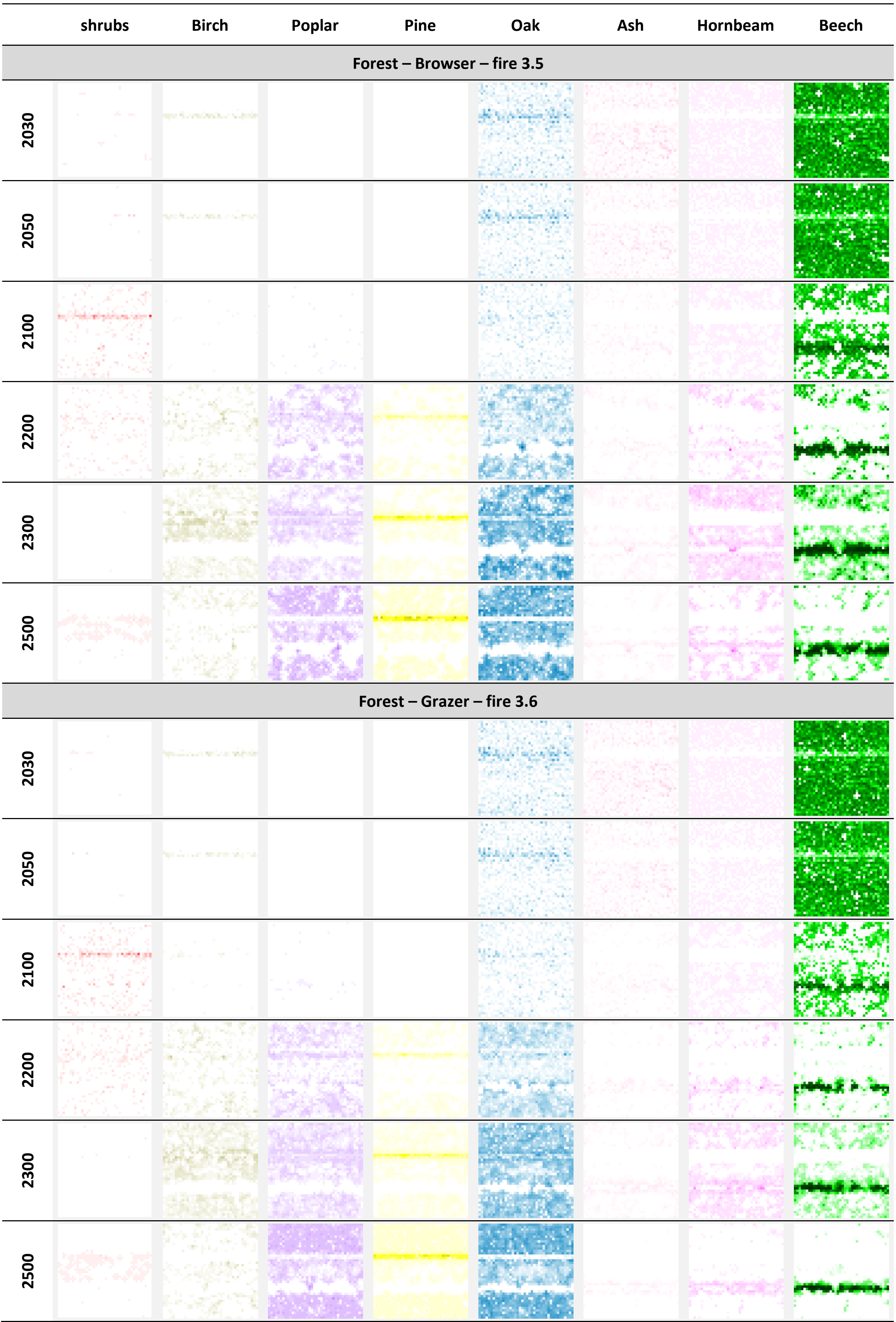
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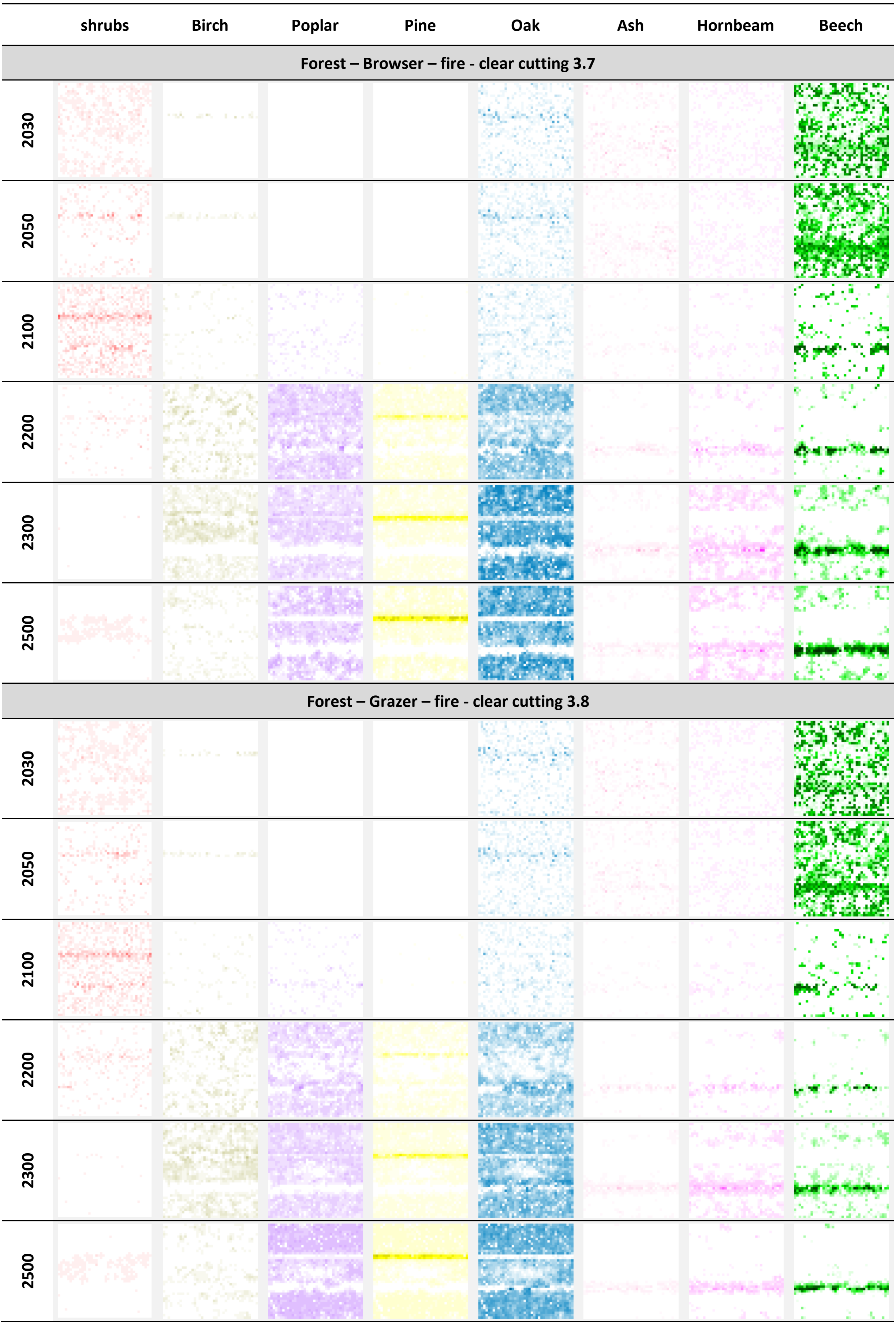
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## 3 Methodological critique and uncertainty analysis

The simulated effects on open landscape driven by large herbivore habitat use and wildfire base on a balance between tree dispersal and growth (progressive succession) and foraging- and disturbance-effects on the vegetation (regressive succession). The **parametrization** of these parameters **referred to observed data, as far as possible**. Nevertheless, in cases of lack of observed data or if process formulations had to be strongly generalized, deductions and estimations had to take place. Therefore, in the following we **discuss remaining uncertainties** from major processes, parameters and plausibility-checks that were documented in detail in the methods.

### 3.1 Establishment and growth of woody plants

The parametrization of tree establishment and tree growth mainly determines the succession dynamics in the open landscape (progressive succession, e.g. encroachment). As well does the regeneration potential from browsing and wildfire (regressive succession). Therefore, the parametrization of the tree species-specific growth potential determines the development of open landscape under browsing pressure. The parametrization of tree species-specific dispersal behavior and competitive strength determines a realistic forest development in the open landscape (e.g. pioneer` followed by shade-tolerant species). Further, it determines the simulation of a realistic regeneration from wildfire and a realistic long-term forest community.

**Growth strength of woody plants**

The spin up simulation reproduced a forest community with beech as the dominant species accompanied by oak, hornbeam, and ash. Additional, pioneer species like birch and rowan occurred. Already after 200 simulation years, the spin up reproduced a dense cover of seedlings representing this realistic forest community. Therefore, the parametrization of tree species-specific growth strength tends to be strong. In case of beech, also the regeneration potential post to disturbances was parametrized as strong, because in simulations beech dominance in the understorey was overestimated.

Altogether, in simulations, the model **overestimated the growth strength and regeneration potential of beech in regards to forest disturbance and herbivore browsing**. Generally, this is also true for the growth strength of other simulated tree species, because the relation among tree species-specific growth strengths determines the (realistic) forest community.

**Dispersal of woody plants**

Simulations of the forest development in the open landscape scenario (Scenario 1.1) under impact of the common herbivore community showed a realistic successional pathway and colonization pattern (Figure 6 and Figure 15). Colonization was initiated with shrub (blackthorn, hawthorn), followed by birch, poplar, and pine. In addition, oak and hornbeam individuals occurred already early. The colonization of birch and poplar has been less observed at the study site. We therefore expect that the in simulations the model overestimated colonization of woody species in the open landscape.

In comparison to observations of the last decades, simulated pioneer forest development was slower and not until the end of the Century reached a cover of more than 20% (Scenario 1.1, Figure 12). The faster progressive tree succession in the last decades might result from a higher availability of disturbed patches and gaps in the vegetation post to military practices. At the study site, several forest stands and thickets occur in a linear pattern. This linear pattern can derive from former vehicles lanes or trenches. Due to rapid tree colonization, the availability of open gaps decreased over time and additional loss of disturbances lead to an increase in progressive fallow succession. This dense grass sward inhibits progressive tree succession. Similar vegetation dynamics have been observed in productive grassland systems (wetland or on loess soils of the Schwäbische Alb). Foraging and trampling pressure of wild large herbivores at low densities is too low to open up the grass sward. (Wild boar has the potential, but was not simulated.) The parametrization of seed dispersal was realistic.

Generally, drought stress during the vegetation period can lead to failures of tree establishment (number of seedlings and juveniles, observation data, Hopf 2017). In regards to climate change-driven drought stress, it can be expected that in case of an extreme climate change scenario, tree succession dynamics in the open landscape will be slower than in our simulations. We only simulated a moderate climate change scenario of rcp4.5, therefore our simulations **overestimate future tree encroachment in the open landscape**.

### 3.2 Large herbivore density and herbaceous forage supply

The relation between large herbivore density and forage supply determines the grazing and browsing pressure on the vegetation at landscape scale.

The simulated density of herbivores derives from scan flights, which are known to document lower number of inidivduals (especially in case of roe deer) due to technical limitations (Franke et al. 2012). Further, we simulated a status quo density, because of the lack of reliable and precise data about population dynamics, although we are aware that herds have increased in the past.

Regarding the productivity of the herbaceous vegetation, we neglect drought-driven productivity decreases. Such climate change-induced effects on forage supply have been demonstrated in wooded pastures in the Jura (Gavazov et al. 2013). The productivity of the fallow grassland vegetation (Figure 11) in the open landscape was based on standard values used in agriculture (Table 3), therefore its productivity was classified quite high.

Altogether, in simulations we underestimate forage demand and overestimate the forage production. In the context of increasing herbivore densities our simulations, **underestimate future grazing and browsing pressure** on the vegetation, especially in view of increased summer drought.

### 3.3 Frequency of wildfires

In simulations, a high threshold value that related to the maximum monthly aridity determined wildfire ignition. Observations of controlled burning experiments in landscape conservation, described that under current climate conditions (e.g. drought) high standing biomass in the grassland showed a high flammability and fire proneness. The high threshold value also evoked that the frequency of simulated wildfires decreased after 2100 AD (in comparison 2050 to 2100 AD).

According to the observations of the historical wildfire events in the Tessin, wildfire ignition was preferentially in times of dry northern föhn winds. However, according to the predicted development of annual mean precipitation rates in the climate change scenario for the Hainich these are less than those currently in the Tessin. Therefore, simulation begin of a wildfire regime in the Hainich could already be earlier than 2050 AD.

Altogether, simulations **underestimated the occurrence of wildfire** and therefore also their effect on landscape openness.

### 3.4 Overview

The following processes have the tendency to be overestimated:

- Tree and shrub establishment in the open landscape
- Growth strength and growth time of tree species, especially the regeneration potential of beech from browsing and disturbance

The following processes have the tendency to be underestimated:

- Foraging pressure on vegetation, especially browsing pressure
- Foraging pressure in times of forage scarcity (summer drought)
- Frequency of wildfires and begin of wildfire regime (occurrence)

Altogether, the progressive successional processes are overestimated and regressive successional processes are underestimated. Consequently, the simulated effects on open landscape have to be considered in a conservative manner. Because in face of increasing herbivore densities and of an extreme climate change, one can expect landscape that is more open.

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